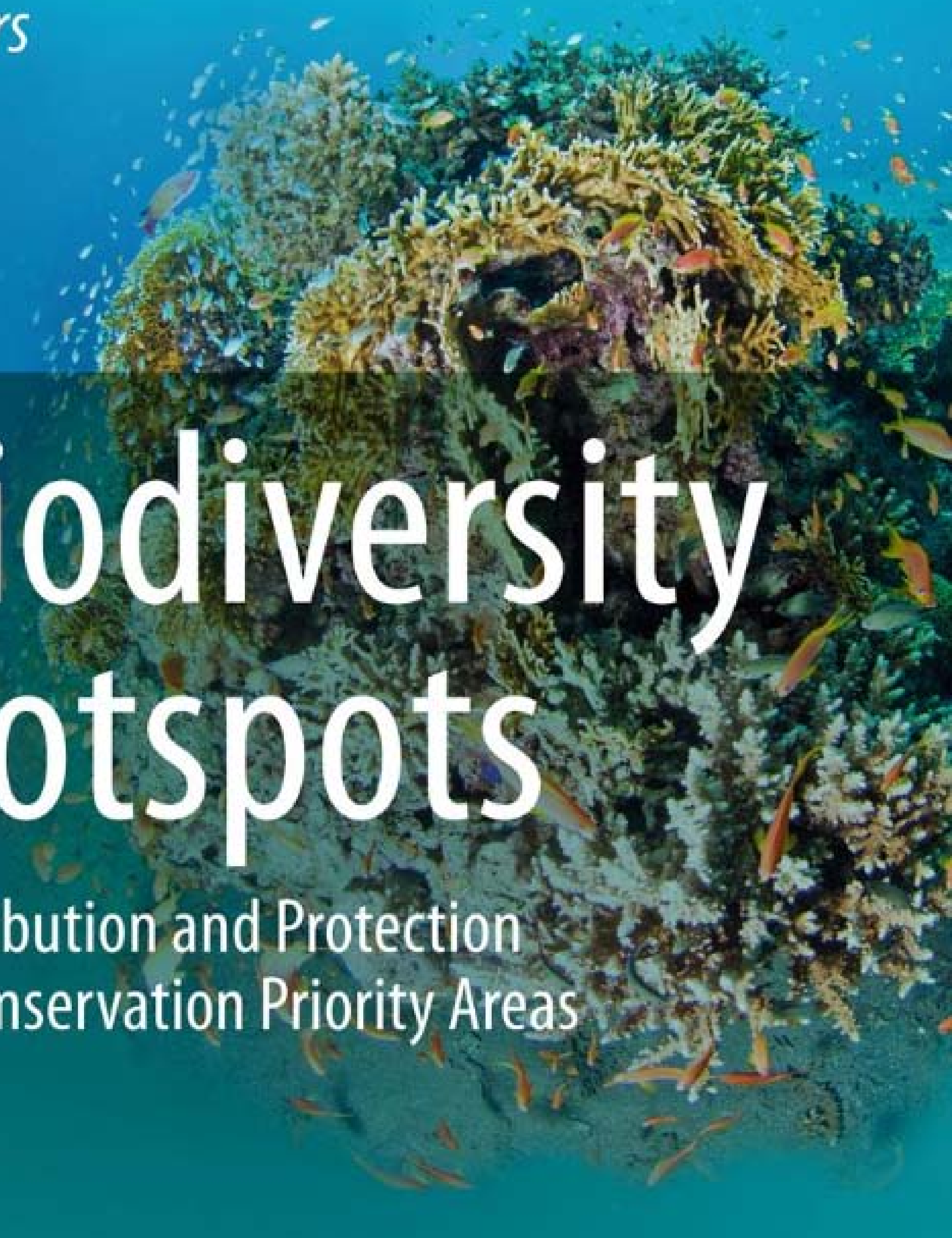

Frank E. Zachos
Jan Christian Habel
Editors

Biodiversity Hotspots

Distribution and Protection of Conservation Priority Areas

Springer

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Front cover: Coral reefs are among the most diverse habitats on the planet. The front cover photograph was taken by Jonas Thormar in the Red Sea and shows a bombora, or isolated piece of reef, near Eilat, Israel.
Back cover: A still-undescribed species of Harlequin frog (*Atelopus* sp.) photographed in the Tropical Andes biodiversity hotspot by Jos Kielgast. This species is on the verge of extinction, as are more than 80% of the members of its large and spectacular genus. Amphibians on the whole are among the taxa suffering most in the present biodiversity crisis.

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Preface

The United Nations declared 2010 to be the International Year of Biodiversity. This declaration highlights both the value of biodiversity and the urgent need to take action preserving it in the light of what has often been called the Sixth Extinction. Already some twenty years ago, E.O. Wilson estimated that about 30,000 species became extinct per year (or, roughly, 3.5 species per hour!). While there has been an ongoing debate about the causes of the first five mass extinctions, there is no doubt about the present one – it is man-made, and there is little reason to believe it will cease in the near future. The IUCN acknowledges three levels of biodiversity: ecosystem, species and genetic diversity, and all three of them are unevenly distributed across our planet. This has led to the concept of biodiversity hotspots, a term that is used with different meanings. While in its strict sense, it is based on a combination of quantified species endemism (at least 1,500 endemic plant species, i.e., 0.5% of all known species) and habitat loss (70% or more of an area's primary vegetation), biodiversity hotspots *sensu lato* refer to any area or region with exceptionally high biodiversity at one or more of the three above-mentioned levels. In this book, unless stated otherwise, this latter usage of the term prevails because it is being applied in both the popular and technical literature (and therefore, it is not feasible to reduce the hotspot term to its technical definition only). The number of acknowledged biodiversity hotspots *sensu stricto* has, over the years, increased from 18 in the late 1980s through 25 in the year 2000 to, until very recently, 34. With the publication of this book, the Forests of East Australia have made it into the list as number 35 (see Chap. 16).

This volume owes its existence to a conference on *Biodiversity Hotspots – Evolution and Conservation* held in Luxembourg in March 2009, where experts from different disciplines and continents presented and discussed topics related to biodiversity, its threats and conservation. While some of the following chapters have their roots in talks given at this conference, this book was never intended to be a "conference proceedings volume". Instead, we aimed at filling gaps and covering a wider range of topics by inviting more international experts to contribute chapters from their area of research. A multi-author volume like this will never be a monolithic and fully coherent book, and we are aware that there are inevitably differences in breadth, depth, scope and quality among chapters. Also, we are sure that some readers may wonder why some region or aspect is considered, while others are not. In a single volume of merely 500+ pages, there will always be a certain degree of contingency with respect to the choice of subjects, and even more so when a topic as colossal as this is tackled. We freely admit that there are still gaps at least some of which, however, are due to the fact that invited authors declined or were not able to contribute a chapter within the time frame of this book. We have been aware of these shortcomings from the beginning, and we have tried to compensate for this by broadening our scope and also including chapters on human diversity, ways of measuring biodiversity and the sociocultural dimension of conservation biology. We are happy to have, apart from the newly described 35th biodiversity hotspot *s. str.*, chapters on classical regions or biotopes of high diversity such as Madagascar, the Mata Atlantica, the Mediterranean or coral reefs, and we were lucky enough to also have a chapter on the deep sea, a realm whose contribution to global biodiversity we are only just beginning to understand. In addition to this, the book contains chapters on particular taxa, among them African cichlid fishes, the textbook example of adaptive radiation and species diversity, amphibians (which are threatened globally) and invertebrates (which are strikingly underrepresented in biodiversity assessments – despite the fact that they account for more than 90% of all species).

Although biodiversity and its conservation are very much en vogue in today's ecological and evolutionary research, we hope that a book like this may still contribute to deepening our knowledge and increasing the awareness for the rapid loss of our most valuable legacy. We are grateful to Springer publishers for the opportunity to edit this volume and to Andrea Schlitzberger and Dieter Czeschlik for their editorial help. Moreover, we thankfully acknowledge the Springer referees who made valuable suggestions and insightful comments during the planning phase of this book, and last but not least we wish to express our gratitude to the peer-reviewers of the single chapters that have helped to improve this book by sharing their knowledge with us.

Kiel, Germany — Frank E. Zachos
Luxembourg, Luxembourg — Jan C. Habel

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Part I
Introductory and Global Aspects

Chapter 1
Global Biodiversity Conservation: The Critical Role of Hotspots

**Russell A. Mittermeier, Will R. Turner, Frank W. Larsen,
Thomas M. Brooks, and Claude Gascon**

Abstract Global changes, from habitat loss and invasive species to anthropogenic climate change, have initiated the sixth great mass extinction event in Earth's history. As species become threatened and vanish, so too do the broader ecosystems and myriad benefits to human well-being that depend upon biodiversity. Bringing an end to global biodiversity loss requires that limited available resources be guided to those regions that need it most. The biodiversity hotspots do this based on the conservation planning principles of irreplaceability and vulnerability. Here, we review the development of the hotspots over the past two decades and present an analysis of their biodiversity, updated to the current set of 35 regions. We then discuss past and future efforts needed to conserve them, sustaining their fundamental role both as the home of a substantial fraction of global biodiversity and as the ultimate source of many ecosystem services upon which humanity depends.

1.1 Introduction

Earth's biodiversity is in trouble. The combination of unsustainable consumption in developed countries and persistent poverty in developing nations is destroying the natural world. Wild lands continue to suffer widespread incursions from

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agricultural expansion, urbanization, and industrial development, overexploitation threatens the viability of wild populations, invasive species wreak havoc on ecosystems, chemical pollution alters biochemical processes in the soil, air, and water, and rapidly spreading diseases jeopardize entire branches of the tree of life (Millennium Ecosystem Assessment 2005; Vitousek et al. 1997; Wake and Vredenburg 2008). As these threats continue unabated, the impacts of climate change multiply. Changing precipitation and temperature, rising and acidifying oceans, and climate-driven habitat loss will disrupt ecological processes, test species' physiological tolerances, turn forests to deserts, and drive desperate human populations toward further environmental degradation (Turner et al. 2010).

Extinction is the gravest consequence of the biodiversity crisis, since it is irreversible. Human activities have elevated the rate of species extinctions to a thousand or more times the natural background rate (Pimm et al. 1995). What are the consequences of this loss? Most obvious among them may be the lost opportunity for future resource use. Scientists have discovered a mere fraction of Earth's species (perhaps fewer than 10%, or even 1%) and understood the biology of even fewer (Novotny et al. 2002). As species vanish, so too does the health security of every human. Earth's species are a vast genetic storehouse that may harbor a cure for cancer, malaria, or the next new pathogen – cures waiting to be discovered. Compounds initially derived from wild species account for more than half of all commercial medicines – even more in developing nations (Chivian and Bernstein 2008). Natural forms, processes, and ecosystems provide blueprints and inspiration for a growing array of new materials, energy sources, hi-tech devices, and other innovations (Benyus 2009). The current loss of species has been compared to burning down the world's libraries without knowing the content of 90% or more of the books. With loss of species, we lose the ultimate source of our crops and the genes we use to improve agricultural resilience, the inspiration for manufactured products, and the basis of the structure and function of the ecosystems that support humans and all life on Earth (McNeely et al. 2009). Above and beyond material welfare and livelihoods, biodiversity contributes to security, resiliency, and freedom of choices and actions (Millennium Ecosystem Assessment 2005). Less tangible, but no less important, are the cultural, spiritual, and moral costs inflicted by species extinctions. All societies value species for their own sake, and wild plants and animals are integral to the fabric of all the world's cultures (Wilson 1984).

The road to extinction is made even more perilous to people by the loss of the broader ecosystems that underpin our livelihoods, communities, and economies (McNeely et al. 2009). The loss of coastal wetlands and mangrove forests, for example, greatly exacerbates both human mortality and economic damage from tropical cyclones (Costanza et al. 2008; Das and Vincent 2009), while disease outbreaks such as the 2003 emergence of Severe Acute Respiratory Syndrome in East Asia have been directly connected to trade in wildlife for human consumption (Guan et al. 2003). Other consequences of biodiversity loss, more subtle but equally damaging, include the deterioration of Earth's natural capital. Loss of biodiversity on land in the past decade alone is estimated to be costing the global economy

$500 billion annually (TEEB 2009). Reduced diversity may also reduce resilience of ecosystems and the human communities that depend on them. For example, more diverse coral reef communities have been found to suffer less from the diseases that plague degraded reefs elsewhere (Raymundo et al. 2009). As Earth's climate changes, the roles of species and ecosystems will only increase in their importance to humanity (Turner et al. 2009).

In many respects, conservation is local. People generally care more about the biodiversity in the place in which they live. They also depend upon these ecosystems the most – and, broadly speaking, it is these areas over which they have the most control. Furthermore, we believe that all biodiversity is important and that every nation, every region, and every community should do everything possible to conserve their living resources. So, what is the importance of setting global priorities? Extinction is a global phenomenon, with impacts far beyond nearby administrative borders. More practically, biodiversity, the threats to it, and the ability of countries to pay for its conservation vary around the world. The vast majority of the global conservation budget – perhaps 90% – originates in and is spent in economically wealthy countries (James et al. 1999). It is thus critical that those globally flexible funds available – in the hundreds of millions annually – be guided by systematic priorities if we are to move deliberately toward a global goal of reducing biodiversity loss.

The establishment of priorities for biodiversity conservation is complex, but can be framed as a single question. Given the choice, where should action toward reducing the loss of biodiversity be implemented first? The field of conservation planning addresses this question and revolves around a framework of vulnerability and irreplaceability (Margules and Pressey 2000). Vulnerability measures the risk to the species present in a region – if the species and ecosystems that are highly threatened are not protected now, we will not get another chance in the future. Irreplaceability measures the extent to which spatial substitutes exist for securing biodiversity. The number of species alone is an inadequate indication of conservation priority because several areas can share the same species. In contrast, areas with high levels of endemism are irreplaceable. We must conserve these places because the unique species they contain cannot be saved elsewhere. Put another way, biodiversity is not evenly distributed on our planet. It is heavily concentrated in certain areas, these areas have exceptionally high concentrations of endemic species found nowhere else, and many (but not all) of these areas are the areas at greatest risk of disappearing because of heavy human impact.

1.2 History of Hotspots

Myers' seminal paper (Myers 1988) was the first application of the principles of irreplaceability and vulnerability to guide conservation planning on a global scale. Myers described ten tropical forest "hotspots" on the basis of extraordinary plant endemism and high levels of habitat loss, albeit without quantitative criteria for the designation of “hotspot” status. A subsequent analysis added eight additional hotspots, including four from Mediterranean-type ecosystems (Myers 1990). After adopting hotspots as an institutional blueprint in 1989, Conservation International worked with Myers in a first systematic update of the hotspots. It introduced two strict quantitative criteria: to qualify as a hotspot, a region had to contain at least 1,500 vascular plants as endemics (>0.5% of the world’s total), and it had to have 30% or less of its original vegetation (extent of historical habitat cover) remaining. These efforts culminated in an extensive global review (Mittermeier et al. 1999) and scientific publication (Myers et al. 2000) that introduced seven new hotspots on the basis of both the better-defined criteria and new data. A second systematic update (Mittermeier et al. 2004) did not change the criteria, but revisited the set of hotspots based on new data on the distribution of species and threats, as well as genuine changes in the threat status of these regions. That update redefined several hotspots, such as the Eastern Afromontane region, and added several others that were suspected hotspots but for which sufficient data either did not exist or were not accessible to conservation scientists outside of those regions. Sadly, it uncovered another region – the East Melanesian Islands – which rapid habitat destruction had in a short period of time transformed from a biodiverse region that failed to meet the “less than 30% of original vegetation remaining” criterion to a genuine hotspot.

Analyses up to now have revealed a set of 34 biodiversity hotspots. These regions collectively hold no fewer than 50% of vascular plants and 42% of terrestrial vertebrates (amphibians, mammals, birds, and reptiles) as endemics (Mittermeier et al. 2004). Because of the extreme habitat loss in these regions, this irreplaceable wealth of biodiversity is concentrated in remaining habitat totaling just 2.3% of the world’s land area (3.4 million km^2; the original extent of habitat in these regions was 23.5 million km^2, or 15.7%).

In contrast with the terrestrial realm, data on the distribution and status of aquatic species are just beginning to be synthesized at a global scale. The publication of a first comprehensive global assessment of conservation priorities for an aquatic system – the coral reef study by Roberts et al. (2002) – has led to much-needed attention on marine hotspots. Our data on marine regions remain sparse compared with information on terrestrial systems (Sala and Knowlton 2006), and our lack of knowledge about freshwater systems is even more pronounced. However, significant strides are being made on aquatic biodiversity, for example, with efforts such as the Global Freshwater Biodiversity Assessment (Darwall et al. 2005) and the Global Marine Species Assessment, which includes comprehensive status assessments completed for reef-forming corals (Carpenter et al. 2008), and similar work under way for many thousands of other species.

The impacts of the biodiversity hotspots on conservation have been diverse and profound. Perhaps the most easily tracked metric is scientific impact. This metric indicates that the hotspots benchmark paper, Myers et al. (2000), has been cited by thousands of peer-reviewed articles, becoming the single most cited paper in the ISI Essential Science Indicators category “Environment/Ecology” for the decade ending 2005. Yet the far more substantive impact has been in resource allocation. Myers (2003) estimated that the hotspots concept focused US$750 million in globally flexible funding over the preceding 15 years. Entire funding mechanisms have been established to reflect global prioritization, among them are the US$235 million Critical Ecosystem Partnership Fund (cepf.net/) and the US$100 million Global Conservation Fund (conservation.org/gcf/; GCF additionally targets high-biodiversity wilderness areas). The ideas have also been incorporated into the Resource Allocation Framework of the Global Environment Facility (gefweb.org/), the largest conservation donor. All told, it is likely that the concept has focused well in excess of US$1 billion on these globally important regions.

The last major hotspots update (Mittermeier et al. 2004) gave “honorable mention” to two other areas, the island of Taiwan and the Queensland Wet Tropics of northeast Australia, which just missed making the hotspots cutoff criteria. However, it was noted that *all* the rain forests of east Australia, and not just the very circumscribed Wet Tropics, should be included as a hotspot, but that data gathering to support this had not yet been completed. That investigation has now been concluded, showing that the region does in fact merit hotspot status, harboring at least 2,144 vascular plant species as endemics in an area with just 23% of its original vegetative cover remaining. This new addition to the hotspots list is detailed in Williams et al. (2011), bringing the total number of hotspots to 35 (Fig. 1.1). Table 1.1 tracks the regions considered biodiversity hotspots from the inception of the concept in 1988 through the various revisions to the present version, which includes the Forests of East Australia Hotspot.

1.3 Hotspots and Biodiversity

As new data enable us to periodically update the hotspots, they also grant us an increasingly complete picture of the natural wealth and human context of these important areas. Here, we examine the current state of our knowledge, building from earlier analyses with updated biodiversity data. The Global Mammal Assessment (Schipper et al. 2008), for example, provides substantially revised data on the status and distribution of Earth’s mammals, while recently compiled population (LandScan 2006) and poverty (CIESIN 2005) data sets provide important socio-economic context.

A total of 35 regions now meet the hotspot criteria, each holding at least 1,500 endemic plant species and each having lost 70% or more of its original habitat extent. Combined, the 35 hotspots once covered a land area of 23.7 million km^2, or 15.9% of Earth’s land surface, just less than the land area of Russia and Australia combined. However, as a result of the extreme habitat destruction in these regions over the past century, what remains of the natural vegetation in these areas is down to just 2.3% of the world’s land area (3.4 million km^2), just greater than the land area of India. More than 85% of the habitat originally present in the hotspots has

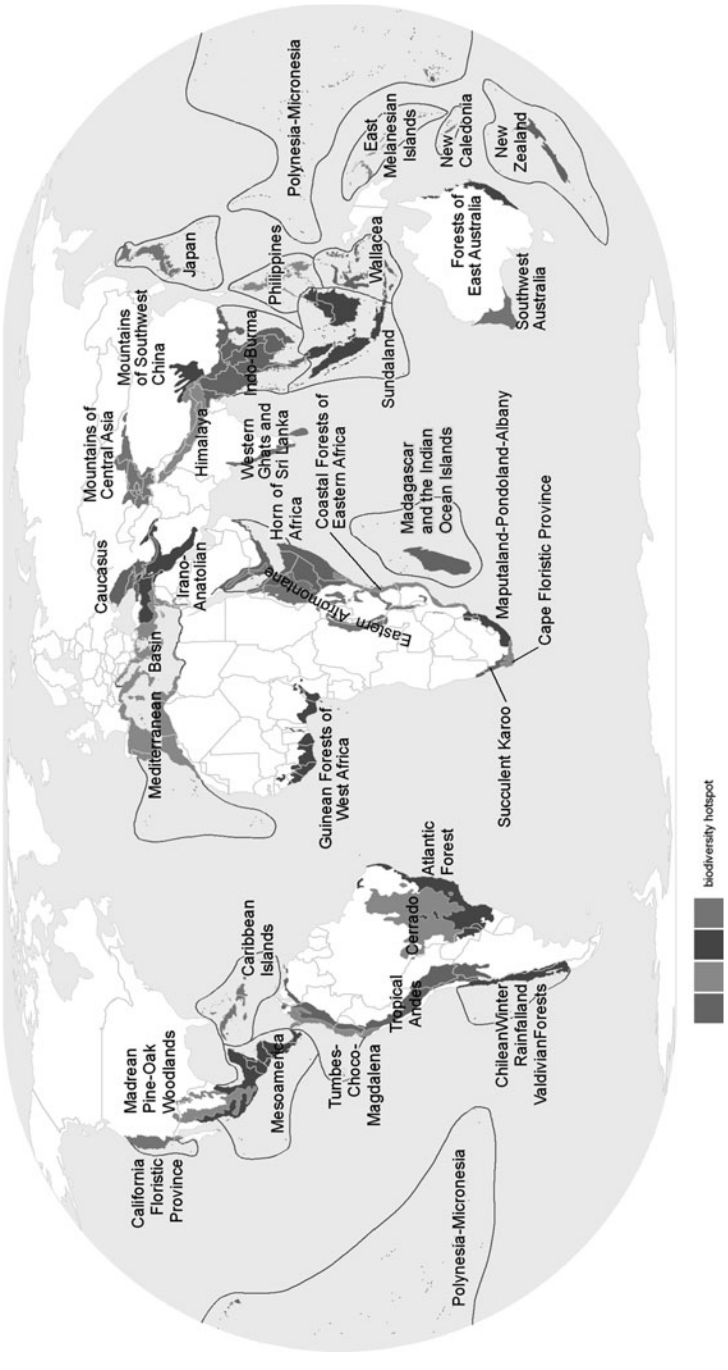

Fig. 1.1 The biodiversity hotspots, Earth's biologically richest and most threatened terrestrial ecosystems. Numbering 35 as of 2011, these include the newly added Forests of East Australia Hotspot

Table 1.1 The biodiversity hotspots from 1988 to present

Myers (1988)	Myers (1990)	Mittermeier et al. (1999)/Myers et al. (2000)	Mittermeier et al. (2004)	2011 Revision
Uplands of Western Amazonia	Uplands of Western Amazonia	Tropical Andes[a]	Tropical Andes	Tropical Andes
Western Ecuador	Western Ecuador			
Colombian Choco	Colombian Choco	Choco/Darien/western Ecuador[b]	Tumbes-Choco-Magdalena	Tumbes-Choco-Magdalena
Atlantic Coast Brazil	Atlantic Coast Brazil	Atlantic Coast Brazil[a]	Atlantic Forest	Atlantic Forest
		Brazilian Cerrado	Cerrado	Cerrado
	Central Chile	Central Chile[a]	Chilean Winter Rainfall and Valdivian Forests	Chilean Winter Rainfall and Valdivian Forests
		Mesoamerica	Mesoamerica	Mesoamerica
			Madrean Pine–Oak Woodlands	Madrean Pine–Oak Woodlands
		Caribbean	Caribbean Islands	Caribbean Islands
	California Floristic Province	California Floristic Province	California Floristic Province	California Floristic Province
	Ivory Coast	Guinean Forests of West Africa[a]	Guinean Forests of West Africa	Guinean Forests of West Africa
	Cape Floristic Region	Cape Floristic Province	Cape Floristic Region	Cape Floristic Region
		Succulent Karoo	Succulent Karoo	Succulent Karoo
			Maputaland-Pondoland-Albany	Maputaland-Pondoland-Albany
			Eastern Afromontane[d]	Eastern Afromontane
	Tanzania	Eastern Arc and Coastal Forests of Tanzania/Kenya[c]	Coastal Forests of Eastern Africa[d]	Coastal Forests of Eastern Africa
			Horn of Africa	Horn of Africa
Eastern Madagascar	Eastern Madagascar	Madagascar and Indian Ocean Islands	Madagascar and Indian Ocean Islands	Madagascar and Indian Ocean Islands
		Mediterranean Basin	Mediterranean Basin	Mediterranean Basin
		Caucasus	Caucasus	Caucasus

(continued)

Table 1.1 (continued)

Myers (1988)	Myers (1990)	Mittermeier et al. (1999)/Myers et al. (2000)	Mittermeier et al. (2004)	2011 Revision
			Irano-Anatolian	Irano-Anatolian
			Mountains of Central Asia	Mountains of Central Asia
	Western Ghats in India			
	Southwestern Sri Lanka	Western Ghats and Sri Lanka[b]	Western Ghats and Sri Lanka	Western Ghats and Sri Lanka
		Mountains of South-Central China	Mountains of Southwest China	Mountains of Southwest China
			Indo-Burma	Indo-Burma
Eastern Himalayas	Eastern Himalayas	Indo-Burma[e]	Himalaya[f]	Himalaya
Peninsular Malaysia	Peninsular Malaysia			
Nothern Borneo	Nothern Borneo	Sundaland[b]	Sundaland	Sundaland
		Wallacea	Wallacea	Wallacea
Philippines	Philippines	Philippines	Philippines	Philippines
			Japan	Japan
	Southwest Australia	Southwest Australia[a]	Southwest Australia	Southwest Australia
				Forests of East Australia
			East Melanesian Islands	East Melanesian Islands
		New Zealand	New Zealand	New Zealand
New Caledonia	New Caledonia	New Caledonia	New Caledonia	New Caledonia
		Polynesia–Micronesia	Polynesia–Micronesia	Polynesia–Micronesia

[a] Expanded

[b] Merged and/or expanded

[c] Expanded to include Coastal Forests of Tanzania and parts of Kenya

[d] The Eastern Arc and Coastal Forests of Tanzania/Kenya hotspot was split into the Eastern Afromontane hotspot (the Eastern Arc Mountains and Southern Rift, the Albertine Rift, and the Ethiopian Highlands) and Coastal Forests of Eastern Africa (southern Somalia south through Kenya, Tanzania and Mozambique)

[e] Eastern Himalayas was divided into Mountains of South-Central China and Indo-Burma, the latter of which was expanded

[f] The Indo-Burma hotspot was redefined and the Himalayan chain was separated as a new Himalayan hotspot, which was expanded

been destroyed. This means that an irreplaceable wealth of biodiversity is concentrated in what is in fact a very small portion of our planet.

Updated data and the addition of the Forests of East Australia Hotspot reconfirm the extraordinary concentration of biodiversity within the hotspots (Table 1.2). The hotspots hold more than 152,000 plant species, or over 50% of the world's total, as single-hotspot endemics, and many additional species are surely endemic to combinations of hotspots. While plant numbers are based on specialist estimates, major advances in the reliability of species distribution data allow much more accurate statistics to be compiled for terrestrial vertebrates (birds, amphibians, mammals, and reptiles). Overall, 22,939 terrestrial vertebrates, or 77% of the world's total, are found in the hotspots. A total of 12,717 vertebrate species (43%) are found only within the biodiversity hotspots, including 10,600 that are endemic to single hotspots and the remainder confined to multiple hotspots. Among individual vertebrate classes, the hotspots harbor as endemics 1,845 mammals (35% of all mammal species), 3,551 birds (35%), 3,608 amphibians (59%), and 3,723 reptiles (46%). If one considers only threatened species – those that are assessed as Critically Endangered, Endangered, or Vulnerable on the IUCN Red List of Threatened Species (IUCN 2008) – we find that 60% of threatened mammals, 63% of threatened birds, and 79% of threatened amphibians are found exclusively within the hotspots. Although reptiles and amphibians show a greater tendency toward hotspot endemism than the generally more wide-ranging birds and mammals, the overall similarity among plant and various vertebrate taxa confirms a general congruence of higher-priority regions across multiple taxa.

Although the concentration of species-level richness and endemism in the hotspots is striking, it is not sufficient to assess the overall biological diversity of the hotspots. It may be that other measures that assess phylogenetic diversity or evolutionary history better represent some aspects of biodiversity – for example, ecological diversity, evolutionary potential, and the range of options for future human use – than does endemism at the species level alone. However, our knowledge of phylogenetic information for entire clades is not yet sufficient for detailed analysis of the evolutionary history found within hotspots or other regions (but see Sechrest et al. 2002). Although the delineation of higher taxa (i.e., Linnean categories) is somewhat subjective, taxonomic distinctiveness should be a useful proxy for evolutionary, physiological, and ecological distinctiveness. Overall, the biodiversity hotspots harbor a disproportionate share of higher taxonomic diversity, holding as endemics 1,523 vertebrate genera (23% of all mammal, bird, fish, reptile, and amphibian genera) and 61 families (9%). This is nowhere more striking than in Madagascar and the Indian Ocean Islands Hotspot, which by itself harbors 175 endemic vertebrate genera and 22 endemic vertebrate families, the importance of which cannot be overstated. Other island systems such as the Caribbean, New Zealand, and New Caledonia harbor tremendous endemic diversity at higher taxonomic levels, as do mainland systems such as the Tropical Andes and the Eastern Afromontane region (Table 1.3).

Although by definition we know little about what future options biodiversity may provide, time and again humanity finds solutions in biodiversity – medicines,

Table 1.2 Plant and vertebrate species occurring in (O) and endemic to (E) each of the biodiversity hotspots

	Plants[a]		Birds[a]		Reptiles[a]		Freshwater fishes[a]		Amphibians[b]		Mammals[c]	
Hotspot	O	E	O	E	O	E	O	E	O	E	O	E
Tropical Andes	30,000	15,000	1,728	584	610	275	380	131	1,095	763	595	117
Tumbes-Choco-Magdalena	11,000	2,750	892	112	325	98	251	115	209	33	277	16
Atlantic Forest	20,000	8,000	936	148	306	94	350	133	516	323	312	48
Cerrado	10,000	4,400	605	16	225	33	800	200	205	34	300	10
Chilean Winter Rainfall and Valdiv	3,892	1,957	226	12	41	27	43	24	44	32	69	19
Mesoamerica	17,000	2,941	1,124	213	686	240	509	340	585	385	418	97
Madrean pine-Oak Woodlands	5,300	3,975	525	23	384	37	84	18	213	59	304	14
Caribbean Islands	13,000	6,550	607	167	499	468	161	65	176	169	65	48
California Floristic Province	3,488	2,124	341	8	69	4	73	15	54	27	141	15
Guinean Forests of West Africa	9,000	1,800	793	75	206	52	512	143	229	88	315	47
Cape Floristic Region	9,000	6,210	324	6	100	22	34	14	47	16	109	0
Succulent Karoo	6,356	2,439	227	1	94	15	28	0	21	1	101	1
Maputal and-Pondoland–Albany	8,100	1,900	541	0	205	36	73	20	73	11	197	3
Costal Forest of Eastern Africa	4,000	1,750	636	12	250	54	219	32	95	10	236	7
Eastern Afromontane	7,598	2,356	1,325	110	347	93	893	617	244	75	510	52
Horn of Africa	5,000	2,750	704	25	284	93	100	10	30	6	189	18
Madagascar and the Indian Ocean l	13,000	11,600	313	183	381	367	164	97	250	249	200	192
Mediterranean Basin	22,500	11,700	497	32	228	77	216	63	91	41	216	27
Caucasus	6,400	1,600	381	2	87	20	127	12	18	3	146	12
Irano-Anatolian	6,000	2,500	364	0	116	13	90	30	20	3	150	9
Mountains of Central Asia	5,500	1,500	493	0	59	1	27	5	8	4	116	7
Western Ghats and Sri Lanka	5,916	3,049	457	35	265	176	191	139	204	156	143	27
Himalaya	10,000	3,160	979	15	177	49	269	33	111	46	269	18
Mountains of Southwest China	12,000	3,500	611	1	94	15	92	23	92	8	237	8
Indo-Burma	13,500	7,000	1,277	73	518	204	1,262	553	328	193	401	100
Sundaland	25,000	15,000	771	146	449	244	950	350	258	210	397	219
Wallacea	10,000	1,500	650	265	222	99	250	50	49	33	244	144

Philippines	9,253	6,091	535	185	235	160	281	67	94	78	178	113
Japan	5,600	1,950	368	15	64	28	214	52	53	46	104	52
Southwest Australia	5,571	2,948	285	10	177	27	20	10	32	22	55	13
East Melanesian Islands	8,000	3,000	365	154	114	54	52	3	50	45	100	44
New Zealand	2,300	1,865	198	89	37	37	39	25	7	4	12	4
New Caledonia	3,270	2,432	105	23	70	62	85	9	0	0	14	6
Polynesia–Micronesia	5,330	3,074	300	170	61	31	96	20	8	3	22	12
Forests of East Australia	8,257	2144.0	632	28	321	70	80	10	120	38	133	6

[a] Hotspot totals for Forests of East Australia from Williams et al. (2011); for all other hotspots from Mittermeier et al. (2004)

[b] Calculated based on species range maps from Stuart et al. (2008)

[c] Calculated based on species range maps from Schipper et al. (2008)

Table 1.3 Hotspots with the greatest total number of endemic higher vertebrate taxa (all mammals, amphibians, birds, freshwater fishes, and reptiles)

	Hotspot (# endemics)	
Rank	Genera	Families
1	Madagascar and the Indian Ocean Islands (175)	Madagascar and the Indian Ocean Islands (22)
2	Eastern Afromontane (119)	Philippines (16)
3	Tropical Andes (103)	Japan (8)
4	Sundaland (97)	Sundaland (7)
5	Mesoamerica (78)	Caribbean Islands (6)
6	Indo-Burma (68)	Chilean Winter Rainfall and Valdivian Forests, Wallacea, New Zealand, New Caledonia (4)
7	Caribbean Islands (65)	
8	Atlantic Forest (63)	
9	Wallacea (62)	
10	Philippines (45)	Mesoamerica, Indo-Burma, and Polynesia–Micronesia (3)

foods, engineering prototypes, and other products – that enhance human lives and address our most pressing problems. It is thus difficult to overestimate the importance of maintaining the option value afforded by the vast storehouse of evolutionary diversity that the biodiversity hotspots represent. This is perhaps nowhere illustrated more clearly than in the case of the gastric-brooding frogs of the genus *Rheobatrachus*. Discovered in the early 1970s amid the streams and forests of Australia, the two *Rheobatrachus* species were the only amphibians known to incubate their young internally, in the mother's stomach. Researchers noted that the compounds secreted to avoid harm to the young might aid the development of treatments for digestive conditions such as ulcers that affect millions of humans worldwide. However, before these possibilities could be explored, the habitats of these unique creatures had become so badly decimated that both species were extinct by the mid-1980s (Hines et al. 1999). As they were endemic to what is now known as the Forests of East Australia Hotspot, failure to conserve them there resulted in their extinction. Redoubled effort is needed in the biodiversity hotspots to ensure that we do not permanently foreclose the opportunity to learn from the evolutionary innovations of other endemic taxa.

Concurrent to the development of the hotspots concept was the recognition of the importance of conserving the least-threatened highly diverse regions of the globe. These high-biodiversity wilderness areas (Mittermeier et al. 2003) are defined on the basis of retaining at least 70% of their original habitat cover, harboring at least 1,500 plant species as endemics, and having a human population density of <5 people per km^2. Based on the updated data used in this analysis, the five High-Biodiversity Wilderness Areas (Amazonia, Congo Forests, Miombo-Mopane Woodlands and Savannas, New Guinea, and North American Deserts) hold 28% of the world's mammals and 20% of the world's amphibians, including 7% of mammals and 11% of amphibians as endemics, in about 7.9% of the world's land surface (6.1% including only intact habitats). While the highly threatened hotspots must be conserved to prevent substantial biodiversity loss in the immediate future, there is also strategic advantage in investing in conserving biodiverse wilderness areas, which by virtue of their intactness and comparatively lower costs make good targets for proactive conservation action (Brooks et al. 2006). For this reason, Conservation International has for the past two decades focused on both the biodiversity hotspots and high-biodiversity wilderness areas as part of its two-pronged strategy for global conservation prioritization.

1.4 Social and Economic Context

The biodiversity extinction crisis is one of several grave challenges facing humanity today. Climate change and the persistence of poverty pose the prospect of a grim future for Earth and billions of its human inhabitants. These challenges, though, are intimately intertwined. The same environmental degradation that threatens the persistence of species contributes substantially to anthropogenic greenhouse gas emissions and undermines the ecosystem services that support human communities. Climate change will have particularly severe impacts on the poor (Ahmed et al. 2009) and jeopardizes a large portion of Earth's species (IPCC 2007; Parmesan and Yohe 2003; Thomas et al. 2004). Yet if these problems are inextricably linked, so too are many solutions. Perhaps nowhere is this more evident than in the hotspots.

The hotspots, home to a major portion of the world's terrestrial biodiversity, are also home to a disproportionate share of its people (Cincotta et al. 2000). Recent population data (LandScan 2006) show that the 35 hotspots contain about 2.08 billion people – 31.8% of all humans – in just 15.9% of Earth's land area (Table 1.4). Populations in hotspots are generally growing faster than the rest of the world. Between the 2002 and 2006 releases of the LandScan population data set, population within hotspots grew an estimated 6.0%, while Earth's overall population increased only 4.8%. Hotspots also contain a substantial fraction of the world's poor. Although spatially explicit estimates of poverty have not been compiled globally, the incidence of child malnutrition provides one measure of the poverty in an area and has been estimated at subnational scales worldwide (CIESIN 2005). These data show that 21% of the world's malnourished children live in hotspots.

The interactions between biodiversity, extreme habitat loss, other threats, and socioeconomic context are complex. Past habitat loss may have indeed been connected to poverty. For example, the lack of alternative sources for food, fuel, shelter, and income can lead to exploitation of natural habitats to meet these urgent needs. Yet rampant consumption of energy, food, and raw materials by both developed and developing countries has played just as great a role in the degradation of these areas, albeit from regions often geographically distant from hotspots. But even this more complete picture misses a critical point. Regardless of past causes, the more pressing issue is that all of humanity depends on the habitats that remain in biodiversity hotspots. Poor communities are often those most dependent on sustaining the clean water, protection from storms, and other ecosystem services they derive from nature. Based on Turner et al. (2007), the estimated value of all services

Table 1.4 Population and poverty in the biodiversity hotspots

	Population 2006	Population density (1 km^{-2})	Malnourished children	Child malnutrition rate (%)
Tropical Andes	57,775,500	38	712,240	8
Tumbes-Choco-Magdalena	14,137,600	52	191,216	11
Atlantic Forest	111,817,000	91	464,519	5
Cerrado	28,011,300	14	160,894	5
Chilean Winter Rainfall and Valdivian Forests	15,285,100	38	11,044	1
Mesoamerica	84,590,400	75	1,493,320	13
Madrean Pine–Oak Woodlands	15,206,500	33	326,133	7
Caribbean Islands	37,516,000	164	214,842	6
California Floristic Province	36,663,100	125	10,744	0
Guinean Forests of West Africa	89,016,200	144	3,466,330	21
Cape Floristic Region	4,269,870	54	27,044	7
Succulent Karoo	372,404	4	3,327	10
Maputaland-Pondoland–Albany	19,598,000	72	179,398	7
Coastal Forests of Eastern Africa	17,024,900	59	822,586	29
Eastern Afromontane	115,799,000	114	8,463,810	38
Horn of Africa	40,017,300	24	2,410,290	31
Madagascar and the Indian Ocean Islands	21,731,700	36	1,345,790	39
Mediterranean Basin	239,517,000	115	899,708	5
Caucasus	37,073,900	69	226,073	9
Irano-Anatolian	51,799,500	58	708,419	11
Mountains of Central Asia	38,005,700	44	444,026	10
Western Ghats and Sri Lanka	51,856,400	275	2,827,980	36
Himalaya	102,492,000	138	5,839,790	40
Mountains of Southwest China	8,739,140	33	40,518	4
Indo-Burma	349,827,000	148	8,855,140	24
Sundaland	229,383,000	153	5,916,330	25
Wallacea	27,861,900	83	638,814	26
Philippines	87,757,400	296	2,846,180	28
Japan	125,347,000	335	0	0
Southwest Australia	1,816,030	5	0	0
East Melanesian Islands	1,284,660	13	0	0
New Zealand	3,935,730	15	0	0
New Caledonia	197,518	10	0	0
Polynesia–Micronesia	2,898,760	62	7,018	5
Forests of East Australia	9,147,190	36	0	0
All 35 hotspots	2,077,771,702	88	49,553,523	21

provided by the hotspots' remaining habitats is $1.59 trillion annually – on a per-area basis more than seven times that provided by the average square kilometer of land worldwide. This calculation is almost certainly an underestimate, as it does not account for the increase in value that may result from the increasing scarcity of these services in hotspots in the face of increasing need for them. Meanwhile, it is not just the poor communities in hotspots that benefit from these services. For example, based on recent data (Reusch and Gibbs 2008), the hotspots store more than 99 Gt of carbon in living plant tissues, and still more in peat and other soils. The greenhouse gas emission reductions that result from slowing high rates of habitat loss in these regions are a critical contribution to slowing global warming.

Hotspots are very important for the survival of human cultural diversity. A study of the distribution of human languages (Gorenflo et al. 2008) used human linguistic diversity as a surrogate for human cultural diversity and found that about 46% of the 6,900 languages still spoken are found within the borders of the hotspots and at least 32% of languages are spoken nowhere else. This concentration very much parallels what we see in terms of endemic species. What is more, it also includes a very high proportion of the languages, and the unique cultures speaking them, most at risk of disappearing over the next few decades.

Hotspots are also notable as centers of violent conflict. Another recent study (Hanson et al. 2009) found that 80% of the world's violent conflicts since 1950 (i.e., those involving more than 1,000 deaths) took place within the biodiversity hotspots and most hotspots experienced repeated episodes of violence over the 60-year span. This result suggests that, if conservation in hotspots is to succeed, conservation efforts must maintain focus during periods of war and that biodiversity conservation considerations should be factored into military, humanitarian, and reconstruction programs in the world's war zones.

1.5 Securing Hotspots for the Future

Threats to hotspots are similar to, although generally more intense than, threats to biodiversity worldwide. Habitat destruction, projected to remain the dominant threat to terrestrial biodiversity even in an era of climate change (Sala et al. 2000), is pervasive in hotspots and driving extinctions in many (Brooks et al. 2002). The growing impacts of climate change will be felt worldwide, as altered precipitation and temperature, rising oceans, and climate-driven habitat loss threaten a large fraction of species with extinction (Thomas et al. 2004) and drive desperate human populations to further environmental degradation (Turner et al. 2010). Other threats are less widespread, but felt severely in particular regions. Introduced predators have devastated island hotspots, where species evolved in the absence of domestic cats and rats and other invasive predators (Steadman 1995). Introduced plants are having massive impacts on hydrology and biodiversity in some hotspots, particularly those having Mediterranean-type vegetation (Groves and di Castri 1991). Exploitation for protein (e.g., bushmeat), for medicine, and for the pet trade threatens species in all hotspots, particularly the Guinean forests of West Africa (Bakarr et al. 2001), Madagascar, and hotspots in Southeast Asia (van Dijk et al. 2000). Chitridiomycosis, a fungal disease, is recognized as a proximate driver of amphibian declines and extinctions worldwide (Stuart et al. 2004; Wake and Vredenburg 2008). It may prove to be the most destructive infectious disease in recorded history, with a substantial effect on the hotspots, which harbor an astonishing 59% of all amphibians as endemics.

The establishment and effective management of protected areas (Bruner et al. 2001) must continue to be the cornerstone of efforts to halt the loss of biodiversity, both in the hotspots and elsewhere. These areas may be in the form of national parks or strict biological reserves or may come in a variety of other forms, depending on local context, including indigenous reserves, private protected areas, and community conservation agreements of various kinds. An overlay of the hotspots with protected areas with defined boundaries from the World Database on Protected Areas (IUCN and WCMC 2009) reveals that 12% of the original area of the 35 hotspots is under some form of protection, while 6% is classified as IUCN category I–IV protected area (which provides a higher degree of protection in terms of constraints on human occupation or resource use). These numbers are underestimates since boundaries for many protected areas have not been systematically compiled, and they certainly overestimate the land area that is managed effectively. Yet the fraction of hotspots covered is less meaningful than the locations themselves. Efforts to conserve the hotspots must focus on ensuring long-term persistence of the areas already protected and strategically add new protected areas in the highest priority unprotected habitats that remain intact as indicated by systematic efforts to identify gaps in protected areas networks (e.g., Rodrigues et al. 2004).

Maintaining the resilience of hotspots in the face of climate change is another major challenge. Changing temperature and precipitation patterns forces species to move according to movement in their preferred habitat conditions, yet these movements will often be both difficult for species to undertake and complex for researchers to predict. Due to the nature of climatic gradients, the distances species must move are likely to be shorter in mountainous terrain and longer in flatter regions (Loarie et al. 2009). On the other hand, mountains are more likely to have habitat discontinuities that make species dispersal more difficult. Meanwhile, species' tolerance to climate variability can be low (Tewksbury et al. 2008) and changing climates are likely to produce a complex global mosaic of climates shifted in space, climates which disappear in the future, and entirely novel climates (Williams et al. 2007). To be successful, then, conservation planning must begin to systematically plan actions in both space and time. Protecting the sites where species currently exist is essential, particularly the Key Biodiversity Areas where species are at greatest current risk (Eken et al. 2004). The hotspots, in fact, harbor 81% of the global total 595 Alliance for Zero Extinction sites – locations harboring the sole remaining populations of the most threatened species (Ricketts et al. 2005). If we lose these sites now, we will not be granted another chance to save their species later. However, this is only the beginning. We must also protect habitats where species will be in the future, as well as provide "stepping stones" to facilitate movement to these new ranges. Biologists are increasing their ability to anticipate and plan for these needs (Hannah et al. 2007). To be successful, conservation in a changing climate will require a very strong focus on ending further habitat destruction as quickly as possible.

1.6 Conclusion

Based initially on plant endemism, the hotspots have in the past two decades been confirmed as priority regions for the efficient conservation of biodiversity more broadly. Collectively, they harbor more than half of all plant species and 43% of all terrestrial vertebrates as endemics, an even greater proportion of threatened species, and a substantial fraction of higher-taxonomic diversity. More recent information has revealed that this phenomenal concentration of biodiversity into habitats covering a combined 2.3% of the world's land area coincides with disproportionate concentrations of ecosystem services in many of the regions where local communities directly depend on the natural environment on a daily basis. While conservation in these areas is made difficult by ongoing threats, scarce information, and limited local financial capacity, conservation here is not optional. Indeed, if we fail in the hotspots, we will lose nearly half of all terrestrial species *regardless* of how successful we are everywhere else, not to mention an almost unthinkably large contribution to greenhouse gas emissions and extensive human suffering resulting from loss of ecosystem services upon which the human populations of the hotspots ultimately depend. Ongoing research reviewed here and in the rest of this volume serves as a rallying cry for greatly augmented funding, research, and political action on behalf of hotspot conservation. The future of life on Earth depends on it.

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Chapter 2
A Tough Choice: Approaches Towards the Setting of Global Conservation Priorities

Christine B. Schmitt

Abstract Owing to limited funding and time, non-governmental organisations, research institutes and intergovernmental conventions developed different approaches to highlighting those regions on earth that most urgently require conservation efforts. The geographic location of these global conservation priorities is to some extent similar or overlapping, and partly contradictory depending on the underlying selection criteria, namely vulnerability, irreplaceability and representativeness; recently, carbon content of ecosystems has evolved as an additional criterion. It is crucial to understand the rationale behind area selection because the setting of priorities is per se a normative issue. This study, therefore, has the objective to compare the selection criteria of the present approaches as a basis for informed decision-making in the field of global nature conservation. While global analyses are important for guiding international conservation strategies, more detailed and specific conservation planning needs to take place at smaller spatial scales considering ecological as well as socio-economic and political factors.

2.1 Introduction

There are many different reasons for nature conservation varying from aesthetic admiration, spiritual awe and scientific curiosity to the tremendous socio-economic benefits provided by functioning ecosystems and their biodiversity (Turner et al. 2007). In the past, protected areas have often been established in an ad hoc manner motivated by lobby groups, politics or simply opportunity. Therefore, conservation efforts often concentrated on remote areas where no conflict of interest occurred, whereas ecosystems with value for commercial uses were overlooked (Chape et al.

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2005; Pressey 1994). Although chance events and plain rationales such as donor wishes, historical relationships and political stability will continue to guide the allocation of conservation funds (Halpern et al. 2006), there has been substantial progress in making conservation planning more science-based and systematic (Carwardine et al. 2009; Margules and Pressey 2000). This is paramount in developing protected area networks that are of adequate size and distribution to cover important parts of the world's biodiversity (Meir et al. 2004; Tear et al. 2005).

Given limited financial resources and time, systematic conservation planning requires the setting of priorities regarding the natural areas where conservation activities should kick off (Naidoo et al. 2006). Such decisions need to be made nationally and regionally and also at the global level because ecosystems and species are not confined within national borders. In fact, nature conservation has become more and more of a global task, and many non-governmental organisations (NGOs), intergovernmental agencies as well as private foundations aim to allocate funding to those regions on earth where conservation activities are most urgently needed (Balmford et al. 2003). They can draw from a wealth of initiatives and approaches developed to identify such global conservation priorities.

To make matters more confusing, however, these initiatives and approaches highlight a diverse range of ecosystems and geographic areas as key for global conservation activities. The plethora of answers as to where protection is most urgently required needs to be viewed against the fact that the setting of priorities is per se a normative issue guided by value judgments and prior decisions about what matters most (Johnson 1995). It is thus crucial to clearly state the rationale for area selection in a transparent manner. This chapter systematically describes and compares the underlying assumptions and criteria of the present approaches with the aim to assist well-founded decision-making in nature conservation at national and international levels.

2.2 Initiatives for the Setting of Global Conservation Priorities

2.2.1 NGO Approaches

In the 1990s and into the early 2000s, environmental NGOs together with scientists and research institutes developed a number of different approaches for identifying the terrestrial ecosystems on earth with the highest conservation priority from a global perspective (Table 2.1). These approaches are largely based on ecological selection criteria and can be grouped into three main categories: proactive, reactive and representative (Brooks et al. 2006).

Proactive approaches prioritise areas of low vulnerability that still harbour large and undisturbed ecosystems. They recommend starting conservation activities before a region is actually threatened such as the remaining pristine rainforests of the Amazon and the Congo basin (Bryant et al. 1997; Mittermeier et al. 2003;

Table 2.1 Proactive, reactive and representative approaches for the selection of biodiversity conservation priority areas at the global level mainly based on a combination of the ecological criteria vulnerability and irreplaceability (see text and Brooks et al. 2006)

Approach	Organisation	Vulnerability	Irreplaceability
Proactive approaches			
Frontier forests (Bryant et al. 1997)	World Resources Institute	Low	Low
Last intact forest landscapes (Greenpeace no year)	Greenpeace	Low	Low
Last of the wild[a] (Sanderson et al. 2002)	Wildlife Conservation Society	Low	Low
Wilderness areas (Mittermeier et al. 2003)	Conservation International	Low	Low
High biodiversity wilderness areas (Mittermeier et al. 2003)	Conservation International	Low	High
Reactive approaches			
Biodiversity hotspots (Mittermeier et al. 2004)	Conservation International	High	High
Alliance for Zero Extinction (AZE) (Ricketts et al. 2005)[b]	52 Conservation organisations	High	High
Key biodiversity areas (KBAs) (Eken et al. 2004; Langhammer et al. 2007)[b]	Conservation International, Birdlife International, Plantlife International	High	High
Important Bird Areas (IBAs) (Birdlife International 2010)[b]	Birdlife International	High	High
Representative approaches			
Centres of plant diversity (Davis and Heywood 1994–1997)	WWF/IUCN	–	High
Endemic Bird Areas (EBAs) (Stattersfield et al. 1998)	Birdlife International	–	High
Global 200 (Olson and Dinerstein 2002)	WWF	–	High
Megadiversity countries (Mittermeier et al. 1997)	Conservation International	–	High

For the measures of vulnerability and irreplaceability, see Tables 2.3 and 2.4, respectively

[a] The "last of the wild" approach is classified as proactive because it puts an emphasis on low vulnerability. At the same time, it also has a representative aspect, because the least vulnerable areas are selected for each biome in each realm on the land surface

[b] Site-specific approaches

Sanderson et al. 2002). In contrast, reactive approaches prioritise areas of high vulnerability and, mostly, of high irreplaceability, e.g., the unique and severely threatened natural ecosystems of Madagascar (Eken et al. 2004; Mittermeier et al. 2004). The underlying principle is that conservation measures are most crucial in those regions on earth which are rich in biodiversity and under immediate threat of destruction. Representative approaches have the objective to highlight all regions considered important for conserving a representative part of the world's biodiversity. Sites are primarily selected for their high degree of irreplaceability without considering site vulnerability. While there is a shared understanding of what vulnerability, irreplaceability and representativeness mean in a descriptive sense, the quantitative characterisation of these terms is not as straightforward and is based on a number of different measures and indicators (see Sect. 2.3).

Most of the presented approaches screen the planet for conservation priorities by applying a predefined set of ecological criteria and generate so-called global conservation priority templates (Brooks et al. 2006). The priority areas are highlighted for their ecological quality not considering the socio-economic and political feasibility of potential conservation actions (see Sect. 2.4). They encompass vast geographic regions, e.g., the 24 “wilderness areas” have a mean size of three million km^2 (Mittermeier et al. 2003), the 34 “biodiversity hotspots” of 700,000 km^2 and the mean size of the 142 terrestrial “Global 200” is 400,000 km^2 (UNEP-WCMC et al. 2008). It is evident that these priority areas cannot be protected as a whole; the aim rather is to draw attention to larger regions that urgently require more detailed assessment and conservation planning at a finer geographic resolution (e.g., Mittermeier et al. 2004; Olson and Dinerstein 2002).

In contrast, the site-specific approaches that have the manageability of an area as an explicit objective prioritise smaller areas, namely the key biodiversity areas (KBAs) and their subsets, Alliance for Zero Extinction (AZE) sites with a median size of 120 km^2 (Ricketts et al. 2005) and the Important Bird Areas (IBAs) with mean sizes varying between 150 km^2, 260 km^2 and 1,700 km^2 in Asia, Europe and Africa, respectively (L. Fishpool, personal communication). While most of the global conservation priority templates were generated for the whole globe at one time, area identification under the site-specific approaches is a continuous process that is still ongoing in many different countries.

2.2.2 International Conventions

Next to the organisation-driven approaches, there are international conventions that deal with the setting of conservation priorities, for instance the Ramsar Convention (adopted in 1971, 159 Parties), the World Heritage Convention (adopted in 1972, 186 Parties) and the Convention on Biological Diversity (CBD) (adopted in 1993, 193 Parties) (Table 2.2). Conventions are binding international agreements with the contracting parties committing themselves to particular tasks and goals as defined in the convention text and during subsequent meetings that take place at regular intervals.

The World Heritage Convention “aims at the identification, protection, conservation, presentation and transmission to future generations of cultural and natural heritage of outstanding universal value” (World Heritage Center 2008). For this purpose, it has established the World Heritage List, which includes 689 cultural, 176 natural and 25 mixed sites in 148 States Parties (February 2010). The Ramsar Convention’s mission is “the conservation and wise use of all wetlands through

Table 2.2 Examples of criteria and obligations related to the selection and management of conservation priority areas under the World Heritage Convention, the Ramsar Convention and the Convention on Biological Diversity

UNESCO Convention concerning the Protection of the World Cultural and Natural Heritage (http://whc.unesco.org/)

World Heritage sites (World Heritage Center 2008)

- Sites of outstanding universal value, i.e., "cultural and/or natural significance which is so exceptional as to transcend national boundaries and to be of common importance for present and future generations of all humanity".
- For example, "the most important and significant natural habitats for in situ conservation of biological diversity, including those containing threatened species of outstanding universal value from the point of view of science or conservation".
- Sites "must have adequate long-term legislative, regulatory, institutional and/or traditional protection" [and] "should have an appropriate management plan".

Convention on Wetlands of International Importance (Ramsar Convention) (http://www.ramsar.org)

Wetlands of International Importance (Ramsar Convention Secretariat 2006)

- Sites containing representative, rare or unique example of wetland types.
- Sites of international importance for conserving biological diversity such as globally threatened species (IUCN Red List), threatened ecological communities, waterbirds, fish and other wetland-dependent species.
- For example, site supports 20,000 or more waterbirds, or regularly supports at least 1% of the individuals in a population of one (sub-)species of waterbirds
- Parties shall promote the wise use of wetlands in their territory, and establish nature reserves on wetlands, whether they are included in the List or not (Articles 3 and 4)

Convention on Biological Diversity (CBD) (http://www.cbd.int)

Programme of Work on Protected Areas (decision VII/28)

- "[. . .] establishment and maintenance by 2010 [. . .] of comprehensive, effectively managed, and ecologically representative national and regional systems of protected areas that collectively [. . .] contribute to achieving the three objectives of the Convention and the 2010 target to significantly reduce the current rate of biodiversity loss".

2010 Target (Provisional framework for goals and targets, decision VII/30)

- Target 1.1: At least 10% of each of the world's ecological regions effectively conserved.
- Target 1.2: Areas of particular importance to biodiversity protected.
- Target 2.2: Status of threatened species improved.

local, regional and national actions and international cooperation, as a contribution towards achieving sustainable development throughout the world" (Ramsar Convention Secretariat 2006). It has established the Ramsar List of Wetlands of International Importance with 1,886 listed sites (February 2010).

When compared with the other two conventions, the CBD has the most comprehensive approach towards the setting of global conservation priorities, since one of its three main objectives basically is "the conservation of biological diversity" (CBD Article 1). It has established seven thematic Programmes of Work for particular ecosystems, a cross-cutting Programme of Work on Protected Areas, and in 2002 adopted the 2010 Biodiversity Target to "achieve by 2010 a significant reduction of the current rate of biodiversity loss". The CBD does not issue a list of priority areas but gives general guidelines on how these areas should be selected at the national level by individual parties (Table 2.2).

The ecological criteria employed by the conventions can be related to the aspects of vulnerability, irreplaceability and representativeness, but each convention has a different focus (Table 2.2). The World Heritage Convention puts much emphasis on irreplaceability in terms of the outstanding universal value of a site. The selection criteria for the World Heritage List are rather intuitive and rely quite strongly on expert opinion (World Heritage Center 2008). In contrast, Ramsar site selection is predominantly based on thorough quantitative criteria that were also used as "role models" in the development of the IBA and KBA concepts (Langhammer et al. 2007; Ramsar Convention Secretariat 2006). The CBD considers all three aspects, but the selection criteria remain at a general level except for the numeric 10% target, leaving room for countries and organisations to develop more specific definitions.

The conventions are an indication for what nation states are willing to commit to in terms of biodiversity conservation priorities and policies at the international level. The agreements are strongly shaped by the political objective of maintaining national sovereignty and have in common that the responsibility for selecting, proposing and managing the sites lies primarily with the contracting parties. As a result, the selection criteria are sufficiently general for individual interpretation at party level (CBD), or they are explicit but the related obligations for countries are rather weak; e.g., the Ramsar Convention uses quantitative criteria in site selection for the Ramsar List, but Parties are not obliged to establish protected areas in those sites (Table 2.2). The World Heritage Convention lists relatively few outstanding sites globally; building successfully on national pride and international prestige most of these sites are legally protected (Magin and Chape 2004).

2.3 Ecological Criteria for the Selection of Global Conservation Priority Areas

The previous section introduced vulnerability, irreplaceability and representativeness as the three main ecological criteria for the selection of global conservation priority areas. However, there is large variability in the indicators used for quantifying or estimating these criteria.

2.3.1 Vulnerability

Vulnerability (or threat, endangerment) refers to the likelihood that an area's biodiversity will be disturbed or lost to current or future threatening processes (Pressey and Taffs 2001). The presented approaches measure vulnerability by

Table 2.3 Measures of vulnerability as defined by the approaches listed in Table 2.1

Approach	Measure
Based on habitat extent and measures of human impact	
Frontier forests	– Forest area: large, primarily forested, natural forest structure, viable populations of typical plant and animal species.
Last intact forest landscapes	– Forest area: >500 km^2, canopy cover >20%, width >10 km without visible sign of significant human impact
Last of the wild	– Human influence index: based on population density, land transformation, accessibility and electrical power infrastructure
(High biodiversity) wilderness areas	– Area $\geq$10,000 km^2 with $\geq$70% of its original habitat intact and population density <5 people/km^2
Biodiversity hotspots	– Area lost $\geq$70% of its original habitat (i.e., historical habitat extent 500 years ago)
Based on IUCN Red List of Threatened Species	
Alliance for Zero Extinction (AZE)[a]	– Site must contain the entire population of at least one endangered (EN) or critically endangered (CR) species
Key biodiversity areas (KBAs)[a]	– Regular occurrence of a globally threatened species at the site in significant numbers, i.e., presence of a single individual for critically endangered (CR) and endangered (EN) species; 30 individuals or ten pairs for vulnerable species (VU).
Important Bird Areas (IBAs)[a]	– Site regularly holds significant numbers of one or more globally threatened species

For references see Table 2.1

[a] Site-specific approaches

quantifying either the extent of remaining natural habitat or the degree of human impact in an area (Table 2.3). In a more indirect way, they also consider an area as vulnerable if it contains globally threatened species according to the IUCN Red List of Threatened Species. Such an internationally well-established and widely accepted threat classification system does not yet exist for threatened habitat or ecosystem types at the global level, but only for particular regions, e.g., the EU priority habitat types (Council Directive 92/43/EEC).

In addition, some approaches rely on expert knowledge or intuition to define vulnerability. For instance, "frontier forests" are defined as "large intact natural forest ecosystems [that are] relatively undisturbed and big enough to maintain all of their biodiversity, including viable populations of the wide-ranging species associated with each forest type" (Bryant et al. 1997). The "centres of plant diversity" are mainly representative approaches, but also take note if experts consider a site as "threatened or under imminent threat of large-scale devastation" (Davis and Heywood 1994–1997).

Most approaches have a specific threshold level to indicate site vulnerability (Table 2.3). This threshold can be set in a way to define high vulnerability, e.g., site contains the entire population of at least one (critically) endangered species (AZE) or to define low vulnerability, e.g., area larger than 10,000 km^2 with at least 70% of its original habitat intact (wilderness areas). In contrast, the human influence index (last of the wild) is calculated as the continuum of human influence across the planet between 0 and 100% at a resolution of 1 km^2. Subsequently, the “last of the wild” are defined as the ten largest contiguous areas with relatively low, i.e., 0–10%, human influence in each biome in each realm (for definition see Olson et al. 2001), with their actual size depending on the spatial pattern of population density and infrastructure. While in some biomes the areas defined as the “last of the wild” are larger than 100,000 km^2, they can be below 5 km^2 in others (Sanderson et al. 2002).

With the exception of some “last of the wild”, habitat-based measures of vulnerability highlight very large areas as conservation priorities. This includes all proactive approaches because their explicit aim is to draw attention to the remaining vast and undisturbed areas at a global scale (Table 2.1). On the contrary, most reactive approaches are based on species-based criteria and highlight smaller and exactly delimited sites for conservation. They are constrained by the fact that adequate data are only available for a limited number of taxa or taxonomic groups, which can render them spatially and taxonomically biased and rather expensive (Cowling et al. 2004; Knight et al. 2007).

2.3.2 Irreplaceability

Irreplaceability (or uniqueness, rarity) is the importance of an area in contributing to a specific set of conservation targets (Pressey and Taffs 2001). While vulnerability has a temporal dimension, e.g., sites with low vulnerability will retain options for conservation in the future, irreplaceability refers to the degree to which geographic (or spatial) options for conservation will be lost if that particular site is lost (Brooks et al. 2006).

In the context of regional conservation planning, irreplaceability is often measured or estimated with complex statistical techniques (see Segan et al. 2010). In contrast, the approaches for the setting of global conservation priorities use simpler definitions or thresholds for irreplaceability (Table 2.4). For instance, irreplaceability is measured by considering the species richness and endemism of the area, or according to the importance of an area for a particular species, such as restricted-range species or congregatory species, e.g., colony-breeding birds.

Measures for irreplaceability that include ecosystem and/or habitat characteristics are less common. With the main emphasis on species richness and endemism, the “centres of plant diversity” also consider some additional criteria, namely having an important gene pool of plants of value to humans, a diverse range of habitat types and a significant proportion of species adapted to special edaphic conditions (Davis and Heywood 1994–1997). The “Global 200” uses a biological distinctiveness index composed of weighted scores for different biodiversity parameters (Table 2.4). Due to regional differences in data availability and in line with the representative character of the approach, this index was compared only within the set of ecoregions sharing the same biome (Olson and Dinerstein 2002). In the case of intactness, the differentiation between vulnerability and

Table 2.4 Measures of irreplaceability as defined by the approaches listed in Table 2.1

Approach	Measure
Based on species richness and endemism	
Biodiversity hotspots, High biodiversity wilderness areas	– Area with >1,500 endemic species of vascular plants (equals 0.5% of the global total)
Centres of plant diversity	– Sites with >1,000 vascular plant species and/or >100 species (=10%) as endemics (for islands >50 endemics or 10% of the flora)
Megadiversity countries	– Countries ranked by species number of higher plants, mammals, birds, reptiles and amphibians
Based on abundance/range of particular species	
Alliance for Zero Extinction (AZE)[a]	– Site is sole area where an endangered (EN) or critically endangered (CR) species occurs, or contains >95% of the EN or CR species' global population for at least one life history segment
Key biodiversity areas (KBAs)[a]	– Site holds ≥5% of the global population of one or more restricted-range species or species with large but clumped distributions, or (seasonally) ≥1% of the global population of a congregatory species [...], or biogeographically restricted assemblages
Important Bird Areas (IBAs)[a]	– Area is one of a set of sites that together hold a suite of restricted-range species or biome-restricted species and/or has exceptionally large numbers of migratory or congregatory species (for specific threshold level see Birdlife International 2010)
Endemic Bird Areas (EBAs)	– Area encompasses the overlapping breeding ranges of two or more restricted-range (<50,000 km^2) landbirds
Including habitat/ecosystem characteristics	
Global 200	– Species richness and endemism, higher taxonomic uniqueness, unique ecological or evolutionary phenomena, global rarity, intactness

For references see Table 2.1
[a] Site-specific approaches

irreplaceability is difficult to make; intactness can refer to low site vulnerability in a temporal sense, but also to site irreplaceability in a spatial dimension if only one intact habitat is left.

2.3.3 *Representativeness*

Representativeness refers to the need for protected areas to represent, or sample, the full variety of habitat types, species assemblages, ecological processes or other natural features that are characteristic for a given region (Margules and Pressey 2000). By definition, representativeness is a very ambiguous criterion because it

Table 2.5 Aspects of representativeness as considered by the approaches listed in Table 2.1

Approach	Aspect
Relative to geographic units	
Last of the wild	Representation of each biome in each realm
Global 200	Representation of characteristic habitat and ecosystem features within each biome in each realm
Relative to global species richness	
Megadiversity countries	Represent the largest part of global species richness
Centres of plant diversity	Represent the most important areas for global plant diversity
Endemic Bird Areas (EBAs)	Represent the most important places for habitat-based conservation of birds worldwide

For references see Table 2.1

strongly depends on the ecological target selected and on the geographic unit considered (Table 2.5).

It can be measured, e.g., in relation to broad, fairly homogeneous biogeographic regions (last of the wild), in relation to characteristic habitat and ecosystem features within each biogeographic region (Global 200) or in relation to national boundaries (megadiversity countries). Other approaches do not define geographic units, but instead measure representativeness according to the species richness of plants (centres of plant diversity) or birds (Endemic Bird Areas, EBAs). A crucial issue is when representativeness is achieved, i.e., how many ecosystems adequately represent all global ecosystems (e.g., Global 200) and which number of species is representative of the global species pool (e.g., megadiversity countries).

The conventions have quite different viewpoints on the issue of representativeness. While the World Heritage Convention was not established to include representativeness in the beginning (Magin and Chape 2004), the Ramsar Convention mentions the importance of representative wetland types (Ramsar Convention Secretariat 2006). The CBD recognises the value of ecologically representative systems of protected areas at national and regional levels. It also puts forward the much debated 10% target for the conservation of the world’s ecological regions (decisions VII/28 and VII/30). Studies that aimed at assessing global progress towards this target illustrate the difficulty of defining representativeness across different ecological scales and geographic units (see Sect. 2.5).

2.4 Socio-economic and Political Factors

While consistent ecological criteria are key in prioritising the globally important areas for biodiversity conservation, consideration of socio-economic and political factors is crucial in setting more specific conservation targets that quantify the amount of a particular biodiversity feature or priority area that can be protected with a given budget (Carwardine et al. 2009; Margules and Pressey 2000). A clear understanding of the economic costs and social constraints related to a particular conservation action will support decision makers in recognising the potential synergies and trade-offs between biodiversity conservation, economic development and societal preferences (Naidoo and Ricketts 2006).

For instance, setting aside an area for conservation usually involves the implementation of commercial use restrictions, which translate into opportunity costs such as timber volume and agricultural production. In addition, there are other kinds of conservation costs such as acquisition costs, ongoing costs associated with management and maintenance, transaction costs, damage costs and the costs of tackling larger-scale threats to the area (Balmford et al. 2003; Naidoo et al. 2006). Since many protected areas restrict not only commercial but also recreational and cultural uses, their successful, long-term implementation depends on societal acceptance, in particular at the local level (Carwardine et al. 2009). Important issues for consideration in this context are the potential availability of conservation area, involvement of local and indigenous communities and selection of the appropriate governance type and level of protection for the prospective protected area (Dudley and Parish 2006). As there are no simple prescriptions for the weighting of ecological and socio-economic criteria, dilemma situations are likely to arise in areas where both biodiversity value and conservation costs are extremely high.

Owing to the difficult issue of national sovereignty, the presented conventions refer to the socio-economic and political aspects of priority area selection in a rather general manner only (see Table 2.2). Besides, none of the global conservation priority templates incorporates relative benefit–cost ratios of conservation into the selection scheme. This is due to the fact that the templates aim at highlighting areas of high biodiversity value independent of the conservation costs, and clearly state that these regions do not represent exact targets for conservation implementation (e.g., Olson and Dinerstein 2002). In addition, there is a lack of spatially explicit economic data that would be appropriate for the use in conservation planning at the global level (Naidoo et al. 2006). Studies that try to compare conservation costs and benefits globally have to rely largely on heuristics and simplistic estimates (Balmford et al. 2003; Wilson et al. 2006).

The site-specific approaches – IBAs, KBAs and AZE sites – put an emphasis on ecological selection criteria and also consider the socio-economic dimension of priority setting, albeit in a rather vague manner. In the case of IBAs, the sites must be amenable for conservation action and management with the aim to get all sites under (inter-)national legal protection (Birdlife International 2010). KBAs are delineated as sites that are, or could potentially be, managed for conservation, while AZE sites should share common management issues; the types of appropriate conservation measure can vary with socio-economic context. Actual conservation planning processes for these sites only start in an ex post manner. The implementation of protected areas or other conservation measures, therefore, lags behind site identification (Eken et al. 2004; Ricketts et al. 2005). In these local and regional level conservation planning processes, it is possible and indispensable to consider measures or estimates of conservation costs and social acceptance (Carwardine et al. 2009; Margules and Pressey 2000; Moore et al. 2004; Pressey and Taffs 2001).

2.5 Distribution and Conservation Status of Global Conservation Priorities

Despite the large amount of data and analyses available, the crucial question where exactly the most urgent conservation priority areas are located globally is still difficult to answer. In total, 79% of the Earth's land surface is identified as a conservation priority at least by one of the global templates (Brooks et al. 2006). Generally, forest ecosystems are of key conservation importance; for instance, all 34 "biodiversity hotspots" and 138 out of 142 terrestrial "Global 200" ecoregions contain at least some forest cover (Schmitt et al. 2009). Furthermore, 83% of the 218 EBAs and 73% of the 234 "centres of plant diversity" are located in forests (WRI 2000).

Amongst the proactive approaches, there is consensus regarding the location of the remaining large and unfragmented landscapes on earth (Brooks et al. 2006). They mostly highlight vast and intact forest landscapes in the boreal zone and in the tropics as well as large desert areas on all continents. The reactive and representative approaches, which include species richness and endemism as predominant selection criteria (see Sect. 2.3), put strong focus on tropical forest ecosystems because these are extremely species rich and, in many cases, also highly vulnerable. This is most obvious regarding the AZE sites that are almost exclusively located in tropical forest (Ricketts et al. 2005); it is also the case for the species-based representative approaches, pointing out the global areas with high plant species (centres of plant diversity), bird species (EBAs) or general species (megadiversity countries) richness. To a lesser extent, Mediterranean ecosystems are highlighted for their outstanding species richness and high vulnerability, e.g., by "biodiversity hotspots" and the "Global 200".

Considering the bias towards the tropics inherent in approaches based on high threat and species richness, habitat-based approaches such as the "last of the wild" and the "Global 200" may be better suited for highlighting a spectrum of the global ecosystems for conservation. Both point out conservation priorities in each biome in each realm; however, the highlighted areas differ substantially (Brooks et al. 2006), because the "last of the wild" approach uses intactness as a selection criterion, while the "Global 200" use the biological distinctiveness index (see Sect. 2.3).

The CBD takes the habitat-based, representative approach one step further. Without relying on additional criteria or indices, the convention postulates that "at least 10% of each of the world's ecological regions [should be] effectively conserved" (decision VII/30). Thus, each type of ecological region globally becomes a conservation priority. While the 10% protection threshold is an arbitrary value and has been much criticised from an ecological point of view, it is an important political target for guiding international conservation commitment (Carwardine et al. 2009; Svancara et al. 2005). It also points to the important issue of how much of the global ecosystems and conservation priority areas are actually formally protected.

This question is explored by gap analyses that evaluate to which extent protected areas represent important biodiversity elements at different geographic scales. The CBD promotes the conducting of gap analyses at the national level (Dudley and Parish 2006) and has stimulated a number of global studies related to the 10% protection target. They assess, for instance, the level of global protected area coverage for different biogeographic units, for conservation priority areas, for threatened species and forest ecosystems (Table 2.6).

Generally, global gap analysis is constrained by incomplete datasets on protected areas and species and by a lack of global consensus on the delineation of different ecosystem types, in particular forests (Schmitt et al. 2009). Despite these shortcomings, global gap analyses can provide crucial information on where on earth the protected area system needs to be expanded further. They show that although the spatial coverage of protected areas has been increasing globally (for an overview see Jenkins and Joppa 2009), there are still many ecological regions and priority areas with inadequate protected area cover. Closing these global conservation gaps requires more detailed systematic conservation planning at national and regional levels that also takes into account socio-economic factors as pointed out above.

2.6 Outlook: Climate Change, Carbon and Conservation Priority Setting

Recently, the prioritisation debate has taken a new turn by considering potential synergies between biodiversity conservation and the maintenance of ecosystem services (Turner et al. 2007). In addition to the established criteria vulnerability, irreplaceability and representativeness, the carbon content of ecosystems, in particular, has become a new criterion for the setting of global conservation priorities and the allocation of global conservation funding (Scharlemann et al. 2010; Strassburg et al. 2010; UNEP-WCMC 2008a). This is due to the important role of natural carbon storage and sequestration in global climate regulation (Gullison et al. 2007).

This issue has received much attention internationally beyond the realm of conservation planning since the discussions on reducing CO_2-emissions from deforestation in the tropics entered the official negotiations of the United Nations Framework Convention on Climate Change (UNFCCC) in 2005. A global mechanism on reducing emissions from deforestation and forest degradation in developing countries (REDD) has been hotly debated since, now called REDD+ due to the inclusion of issues such as conservation, sustainable management of forests and

Table 2.6 Recent studies on protected area gap analysis, which highlight global biodiversity conservation priorities based on assessment of the existing protected area coverage of different biogeographic units, threatened species or priority areas

Assessment of protected areas coverage for:	Brooks et al. (2004)	Rodrigues et al. (2004)	Ricketts et al. (2005)	Chape et al. (2005)	Hoekstra et al. (2005)	Soutullo et al. (2008)	UNEP-WCMC (2008b)	Coad et al. (2009)	Jenkins and Joppa (2009)	Schmitt et al. (2009)
WWF realms[a]	x							x	x	x
WWF biomes[a]	x				x			x	x	
WWF ecoregions[a]					x	x	x	x	x	x
Countries							x			
Other geo-graphic units[b]				x			x			
Forest ecosystems										x
Biodiversity hotspots[c]						x				x
Last of the wild[c]						x				
High biodivers. wilderness areas[c]										x
Global 200[c]						x	x	x		x
AZE sites[c]			x							
Threatened species	x	x								

[a] See Olson et al. (2001)

[b] For example, regions defined by the IUCN World Commission on Protected Areas (WCPA), Udvardy biomes and major habitat types

[c] For references see Table 2.1

enhancement of forest carbon stocks (Pistorius et al. 2010). With approximately 1.5 Gt of carbon emitted annually from the clearing and degradation of tropical forests (Gullison et al. 2007), the rationale is that developing countries will be compensated if they succeed in reducing their emissions of greenhouse gases resulting from such activities. The REDD+ mechanism is likely to be included in a post-2012 climate regime and could lead to unprecedented new financing inter alia for tropical forest conservation. Yet, the extent to which the implementation of REDD+ will have a positive impact on biodiversity conservation depends on pending decisions regarding its scope, definitions, reference levels, leakage and financing (Harvey et al. 2009; Miles and Kapos 2008; Pistorius et al. 2010).

Encouraged by the ongoing negotiations on REDD+, there are many initiatives to identify priority areas that can serve both climate change mitigation and biodiversity conservation. The greatest opportunities for synergy lie in tropical forest areas, where the overlap of high biodiversity and high ecosystem service value including climate regulation is highest (Strassburg et al. 2010; Turner et al. 2007; UNEP-WCMC 2008a). So far, assessment of the spatial relationship between areas high in biodiversity and high in carbon is constrained by uncertainties. For instance, global data for carbon storage in terrestrial ecosystems have rather low resolution and are largely based on estimates (UNEP-WCMC 2008a). Besides, the measurement of carbon stored in above and below ground biomass is quite advanced, but there is a lack of agreement on the value of different ecosystems for carbon sequestration and the magnitude of soil carbon fluxes following land-use change (Strassburg et al. 2010). It is also important to keep in mind the implications of a narrow focus on high carbon and high biodiversity areas, especially if biodiversity is simply measured in terms of species richness.

For instance, the Amazon and the Congo basin have simultaneously high carbon densities and species richness, but relatively few restricted-range or threatened species (Strassburg et al. 2010). Furthermore, there is a risk that the implementation of a carbon-focused REDD+ mechanism might accelerate the conversion and degradation of biodiversity-rich but relatively carbon-poor regions, because conservation investment will be directed away from them while human pressure is likely to increase, as carbon-rich areas become the focus of conservation attention (Miles and Kapos 2008). Areas potentially at risk include some “biodiversity hotspots” (see Sect. 2.2.1) that have outstanding species richness but are relatively carbon poor such as the Brazilian Cerrado, the Cape Floristic province, and the Succulent Karoo in Southern Africa (Strassburg et al. 2010). Finally, the debate on REDD+ bears the danger of neglecting the fact that temperate and boreal forests might not be as species rich as tropical forests but also important in terms of carbon (e.g., Keith et al. 2009).

Similar to the global conservation priority templates presented above, global overlays of high carbon and high biodiversity areas can only give a general overview of where conservation actions are needed most. More detailed conservation planning needs to take place at smaller spatial scales taking into account the whole range of ecological, socio-economic and political factors. The national REDD+ strategies that are currently being developed by many countries bear the potential to establish comprehensive land-use planning programmes that use the different global to site-specific information on conservation priority areas to establish national biodiversity objectives and facilitate the implementation of conservation measures on the ground (Pistorius et al. 2010).

2.7 Conclusions

Attempts to decide which of the presented approaches for the setting of global conservation priorities is the optimal one will certainly create stalemate situations. Although the employed selection criteria are mostly governed by scientifically defendable threshold levels, the prior assumptions about "what" is important are of normative and philosophical nature. It is hardly possible to prove in a broader sense that economic value stands above intrinsic value of an ecosystem or to decide on which threatened species and ecosystems deserve continued conservation action and which ones do not. Similarly, it is difficult to weigh the conservation of the outstanding against the conservation of the representative.

The emotional nature of value judgements underlines that the different approaches are complementary. As illustrated by the variety of measures for irreplaceability, vulnerability and representativeness, the complex distribution pattern of global biodiversity in terms of genes, species and ecosystems inhibits an easy "one size fits all" solution for priority setting. Each approach thus highlights a critical aspect of global biodiversity. Together with the protected area gap analyses, they form a profound data basis on the distribution and conservation status of the earth's ecosystems and species. The variety of global priorities also offers the opportunity to serve the different individual preferences of private and public stakeholders who are willing to provide funding for conservation action on the ground.

The environmental conventions demonstrate that the international community increasingly recognises the value of the whole range of ecosystems globally. While earlier conventions focus on outstanding sites or specific ecosystems such as wetlands, the CBD highlights a variety of ecosystems and puts much emphasis on the representativeness of global conservation action. This bears the advantage that each nation state is assigned a responsibility to contribute towards a common global objective.

It is crucial that global prioritisation and gap analysis are followed up by work at regional and national scales. These are the critical levels for implementing conservation measures, because the implementation process needs to consider particular economic, social and political constraints and the effectiveness of existing protected areas. While this study has shown that there is a wealth of expertise regarding area prioritisation and systematic conservation planning, one remaining challenge is the development and implementation of cost and time efficient monitoring systems for biodiversity conservation that can make sure that the conservation objectives are achieved and maintained in the long run.

Finally, global climate change adds further challenges to the selection of priority areas for conservation. The evolving REDD+ mechanism has the potential to generate unprecedented funding for tropical forest conservation and sustainable land use management in developing countries. It is paramount that the existing approaches for the setting of conservation priorities are considered in national REDD+ strategies to maximise the synergies between emission reduction objectives and biodiversity conservation. At the same time, global climate change creates an enormous uncertainty regarding the future geographic distribution of species and ecosystems. With this in mind, the habitat-based representative approaches towards priority setting bear some advantages. It is likely that attempts to maintain a large and representative variety of functioning ecosystems globally will increase chances for successful climate adaptations. Besides, incorporating the issue of representativeness into conservation planning can stimulate the creation of larger and better connected protected area systems and the exploration of conservation solutions beyond protected areas.

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Chapter 3
Quantifying Biodiversity: Does It Matter What We Measure?

T. Jonathan Davies and Marc W. Cadotte

Abstract The pace and severity of the current extinction crisis is unprecedented, and there is a large disparity between the scale of the problem and the available recourses with which to mitigate it. Prioritising conservation efforts is therefore critical. With the extinction of species, we lose not only taxonomic diversity but also the ecosystem services they provide and the evolutionary history represented on the branches of the tree of life from which they subtend. How we value these alternative currencies of biodiversity might influence global conservation strategy and resource allocation. Fortunately, different currencies frequently covary closely, for example, maximising species richness will also do well at capturing evolutionary history. Nonetheless, differences exist at the margins, and these can have significant impact on ordering conservation priorities. Further, costs also vary and some currencies rank similar attributes differently (e.g., extinction risk versus latent risk). Conservation biologists must be prepared for the difficult choices that lie ahead.

3.1 Introduction

The term *biodiversity* was formally defined at the 1992 United Nations Conference on Environment and Development in Rio de Janeiro as “*the variability among living organisms from all sources, including, ‘inter alia’, terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems*”. More recently, biodiversity has become a catch-all – frequently used in the conservation

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literature to represent any one of multiple levels of biological complexity, from individual genes to ecosystem processes (see Ferrier 2002). Whatever the precise definition, as species are lost through extinctions, so too will be additional components of biodiversity, including the associated ecosystem services they provide, and the millions of years of unique evolutionary history they represent.

Current species extinction rates are estimated to be over an order of magnitude greater than background rates (Pimm et al. 1995) and are projected to increase further over the next several decades if current trends continue (Mace et al. 2005). The terrestrial environment is now dominated by people – approximately 1/3 of land area has been transformed for human use (Vitousek et al. 1997) and 1/4 of global productivity diverted to human consumption (Haberl et al. 2007). The main direct human-induced drivers that impact biodiversity now are habitat loss and fragmentation; whereas climate change is likely to become a dominant future driver, with up to 37% of species projected to be committed to global extinction by 2050 under some scenarios (Thomas et al. 2004). In mammals, perhaps the best-studied clade, 21% of species are currently listed as threatened with extinction by the International Union for Conservation of Nature, an alarming statistic that is echoed across other clades for which we have equivalent information, including birds, amphibians, and plants (http://www.iucnredlist.org/). It is clear that, at least in the short term, the future of biodiversity will largely be shaped by our ability to reduce the rate at which species are being lost.

It is now generally accepted that systematic conservation planning should focus on areas rather than species (Margules and Pressey 2000). However, conservation spending remains below that required to maintain even the currently inadequate network of reserves and protected areas (James et al. 2001; Halpern et al. 2006). Priority setting is, therefore, critical – identifying biodiversity hotspots allows us to focus scarce conservation resources so as to maximise conservation returns (Myers et al. 2000). Although hotspots most typically refer to centres of species richness and endemism in the conservation literature, we here use the more inclusive definition of biodiversity to also consider evolutionary history and functional diversity. In this context, hotspots simply represent areas that capture a disproportionate amount of biodiversity for their area. Identifying hotspots for conservation prioritisation requires placing a value on the units of conservation concern, typically species, summing values within competing areas, and assigning conservation rankings accordingly.

Here, we briefly introduce some challenges in assigning conservation priorities, focusing on hotspot approaches aimed at maximising protection of species richness. We then discuss various alternative biodiversity metrics with particular emphasis on measures that consider the evolutionary history of species. Last, we illustrate how the choice of metric might influence the conservation decision making process, and consider some additional criteria important in conservation triage, such as costs.

3.2 Conservation Prioritisation and Species Richness

Given a set of sites with varying but overlapping species composition and the goal to maximise the number of protected species, identifying the site of greatest conservation worth might seem trivial – simply sum the number of species in each site and pick the one with the highest count. However, even this most simple scenario makes two critical assumptions (1) we have complete information on species distributions and (2) the population sizes and ecological health of a species is equivalent in each of the sites in which it is found. If we now wish to select two or more sites, additional factors must be considered, for example, whether costs are equal between sites and whether a single site is sufficient for ensuring long-term persistence of a species. Further, when selecting a subset of sites from many possible sites, the order in which sites are selected matters. For example, sites ranked two and three in order of total species richness might, in combination, capture more species than simply picking the top two sites (Kirkpatrick 1983; Margules et al. 1988) – the processes by which sites are selected to maximally capture diversity (or minimise the sum of unrepresented diversity) has been termed "complementarity" (Vane-Wright et al. 1991) and is an important component of reserve selection (Pressey et al. 1993). An increasingly sophisticated set of algorithms have been developed to facilitate reserve selection, considering costs as well as benefits (e.g., Pressey et al. 1997; Margules and Pressey 2000; Sarkar et al. 2006). Nonetheless, or perhaps because of this complexity, views on "effectiveness" of prioritisation schemes may differ even when the same data are considered (e.g., Rodrigues 2007 and Grenyer et al. 2006, 2007).

Whilst biodiversity can be quantified in many ways, species richness remains the most commonly used metric (see Gaston 2000; Bonn and Gaston 2005; Fleishman et al. 2006). Species counts offer several pragmatic advantages as follows.

- Species richness can be easily compared between different sites and conservation schemes.
- There already exists detailed information on species richness within many regions.
- Species represent identifiable entities that can be useful for garnering public support and leveraging conservation funds.
- Species provide a focus for policy and legislation (e.g., IUCN; Convention on Biological Diversity, CITES, US Endangered Species Act).

Further, species provide a surrogate for unmeasured genetic and functional diversity. For example, empirical data indicate that species-rich communities tend to be more productive (Cardinale et al. 2006; Worm et al. 2006), although the mechanisms remain debated and might differ with taxon and system (Cardinale et al. 2006, 2007). Theory and experimental data also suggest community stability increases with the number of species because of greater potential for redundancy in links within the community food web (e.g., Naeem and Li 1997; Tilman et al. 1997; Allesina et al. 2009). However, richness counts also have shortcomings.

Critically, hotspots of species richness for one taxon might correspond poorly with hotspots in the richness of another. At biogeographical scales, species richness of higher taxa frequently covaries closely, most evident in the latitudinal diversity gradient (Hillebrand 2004) and can be explained by similar sets of climate and environment variables (Currie et al. 2004). Unfortunately, congruence at finer spatial scales, at which practical conservation acts, may be much lower (van Jaarsveld et al. 1998; Grenyer et al. 2006).

In addition to problems associated with taxonomic congruence, deriving precise estimates of species richness is not always straightforward. Richness counts may be susceptible to sampling biases (Gotelli and Colwell 2001; Hurlbert and Jetz 2007), and species boundaries may be difficult to determine among more closely related lineages (May 1988). Taxonomic inflation – the trend for increasing species diversity via changes to taxonomic nomenclature rather than biological data (Isaac et al. 2004) – can impact conservation decision making and reduce the utility of species lists in conservation planning (Hey et al. 2003; Mace 2004; Isaac et al. 2004; Meiri and Mace 2009). Recent advances in molecular sequencing technology might provide one solution, particularly for less well-studied groups, including microorganisms, where species concepts are vague and morphological data lacking (Blaxter and Floyd 2003; Sinclair et al. 2005). In addition, molecular markers, for example, as DNA-barcodes, may facilitate species identification by non-taxonomists, and aid in the discovery of cryptic species (Savolainen et al. 2005; Smith et al. 2008). Molecular data not only allows us to construct DNA taxonomies sensu Tautz et al. (2003), but provides additional information on species evolutionary relationships, which might also be useful for informing conservation decision making as we discuss below.

3.3 Alternative Biodiversity Metrics

3.3.1 Extinction Risk

Whilst retaining a focus on species-based metrics, we might additionally consider species vulnerabilities, and up-weight species most at risk of imminent extinction. The IUCN Red List of Threatened Species (http://www.iucnredlist.org/) was designed for this purpose. For mammals, the Red List is nearly complete, with species placed in one of the following extinction risk categories, in order of least to most concern: least concern (LC), near-threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR), extinct in the wild (EW), and extinct (EX). Species allocated to one of the latter categories are most likely to be lost the soonest, and it is possible, with care, to convert Red Listings into a quantitative estimate of extinction risk (e.g., Isaac et al. 2007; Redding and Mooers 2006; Mooers et al. 2008; Mace et al. 2008). The global distribution of threatened species richness can be mapped, as for total species richness (e.g., Orme et al. 2005;

Cardillo et al. 2006; Schipper et al. 2008). It is a cause for concern, that when compared, hotspots of species richness are not necessarily congruent with hotspots of threat (Orme et al. 2005).

A complementary approach might be to focus on species that are marching towards extinction at the fastest pace. Time series allow identification of species that are most rapidly traversing the Red List criteria (Butchart et al. 2004). Because to reduce extinctions, the rate of decline must first be reduced, changes in species Red Listings can be used to evaluate conservation successes as well as define conservation goals, such as The 2010 Biodiversity Target, *to achieve by 2010 a significant reduction of the current rate of biodiversity loss*, set by the Convention on Biological Diversity (http://www.cbd.int/2010-target/) (Butchart et al. 2005; Mace and Baillie 2007). An alternative approach might be to focus on species with currently low risks, but which might be vulnerable in the future. Comparative analyses using information on species phylogeny, biology and current threat can identify species whose biology may predispose them to decline rapidly if threats intensify (Cardillo et al. 2006; Purvis 2008). Small geographic range, low abundance, and ecological specialism are often associated with high risk (Fisher and Owens 2004). Across mammals, species most vulnerable to extinction are those that wean at a late age, require large home ranges, live at low population densities and have small geographical ranges that overlap with high human population densities (Cardillo et al. 2008). By using the discrepancy between a species' current extinction risk and that predicted from biology, it is possible to identify regions with high "latent risk" – where many species have biological traits that make them vulnerable to drivers of extinction, such as habitat modification, but where impact is currently low (Cardillo et al. 2006).

3.3.2 The Evolutionary Future

Although anthropogenic changes to the environment are most acutely manifest in species' extinctions, evolutionary futures might also be impacted (Barraclough and Davies 2005). In the near-term, changes in population abundance, connectivity and extent might influence adaptive responses (Mace and Purvis 2008). For example, habitat fragmentation and transformation might reduce gene flow between populations, whereas species introductions and translocations may break-up locally adapted gene complexes. Conservation management and practice has long been cognisant of such concerns, for example, connecting isolated reserves with dispersal corridors (Soulé and Simberloff 1986), and giving protection to "distinct population segments" (e.g., US Endangered Species Act). In the longer term, we might also consider future speciation.

Myers and Knoll (2001) (see also Cowling and Pressey 2001) suggested that conservation goals should be extended to consider the evolutionary future of biodiversity. For example, we can identify clades that have recently diversified and the regions in which they are found. These lineages or areas might represent evolutionary cradles, and therefore deserve higher weighting for conservation prioritisation. However, past success may be a poor indicator of future performance because of the contingent nature of the evolutionary process (de Queiroz 2002). The propensity to diversify is a highly labile trait, and different lineages have radiated at different times. The fossil record is replete with evidence of formerly diverse clades that have since gone extinct or are represented by only a handful of extant species, for example, within mammals multituberculates, plesiadapiforms and primitive ungulates diversified at the K/T boundary and then declined or went extinct early in the Cenozoic (Alroy 2000). Extant mammal species richness is largely a product of relatively recent radiations within a subset of lineages (Bininda-Emonds et al. 2007). Lineages that have prospered over the past few millions of years are most likely those that happened to possess the right set of traits for the environments in which they are found given recent climates (Davies et al. 2004) and, as a corollary, centres of diversification are, in part, a product of the traits that characterise the lineages within them (Davies and Barraclough 2007).

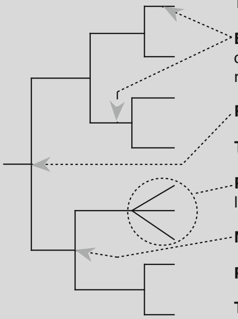
Even if we were able to resolve the interaction between traits and environment that explains past successes, it is difficult to project forward to identify the lineages and regions which might be the cradles of future diversity because we do not have information on future environments. Long-term climate forecasting models suggest the emergence of novel climates with no current analogue, whilst many existing climates will shrink in size (Williams et al. 2007). Predicting the evolutionary future is, therefore, hampered by large uncertainty regarding the magnitude and form of environmental change, and lineage-specific responses (Jablonski 2001). In addition, anthropogenic environmental change and extinctions are occurring on the order of 10–100s of years, but times to speciation are frequently estimated in 1,000−1,000,000s of years (Barraclough and Davies 2005). The timescale for speciation is, therefore, too great for practical management. A precautionary approach to safeguard the evolutionary future would be to maintain a set of species that is overdispersed with respect to their ecological adaptations, maximising the possibility of having the right set of features in an uncertain future (Barraclough and Davies 2005; Davies et al. 2008). Quantifying variation simultaneously across multiple traits and species would be an almost impossible task; fortunately, we can use a simple proxy – phylogeny.

3.3.3 Evolutionary History

If we expand our focus to consider additional attributes of biodiversity, we might value some species over others, for example, because they contribute greater trait or ecological diversity, but this requires detailed species-specific knowledge of physiology and ecology, data that is available for only a small subset of species. Because species tend to diverge over time such that more distantly related species are less similar to each other than more closely related species, the evolutionary distance separating species can be used as a surrogate for the many unique evolutionary and ecological species attributes for which we lack direct measures (Faith 1992; Crozier 1997). Quantifying the evolutionary distinctiveness of a species requires only information on its phylogenetic placement (and that of the other species within the clade of interest – see Box 3.1 for phylogenetic terminology). Species with few close relatives are typically given more weight, as they are assumed to possess more unique features or ecologies that are shared among fewer species (Vane-Wright et al. 1991). Critically, evolutionary relationships may additionally be important in shaping the functional ecology of communities and the ecosystem services they provide (Cadotte et al. 2008) because phylogeny reflects the integrated phenotypic differences among taxa (Harvey and Pagel 1991; Faith 1992; Crozier 1997) and may be a more encapsulating attribute than singular, discretely measured traits (Vane-Wright et al. 1991).

The evolutionary distinctiveness of a species describes its "nestedness" within a phylogenetic tree, and can, for example, be measured as the number of evolutionary divergences (evolutionary splits or nodes) from the root to the respective tip in the phylogenetic tree (see Box 3.1). More nested species (characterised by many splits from root to tip) have many close relatives and are less evolutionarily distinct. Vane-Wright et al. (1991) provided the first quantitative valuation of taxonomic distinctiveness (TD) for conservation – formulation here follows Redding et al. (2008):

Box 3.1. Phylogenies: Representation and Terms



Tree: a figure depicting the phylogenetic relationships among taxa.

Edge (or branch): line orientated along the tip-to-root axis (see below) connecting nodes in the tree. Edge lengths (i.e., time, genetic or trait differences) represent the distance between nodes.

Root: basal edge, represents the common ancestor to all species in phylogeny.

Tip: an extant species subtended by a terminal edge.

Polytomy: unresolved sequence of speciation events, with three or more lineages originating from the same node. A fully resolved tree is bifurcating.

Node: The point where a lineage splits.

PD: phylogenetic diversity – the summed distances of all edges in the phylogeny.

Taxon sampling: the number of included lineages relative to the total number of extant taxa, and its impact on phylogenetic topology and PD.

$$\mathrm{TD}\,(T,i)=\frac{1}{\sum_{v\in q(T,i,r)}\deg_{\mathrm{out}}(v)},\tag{3.1}$$

where, for a tree, T, the set $q(T,i,r)$ includes the node splits between species i and the root of the tree, r. The value of $\deg_{\text{out}}(v)$ for any node is 2 in a perfectly resolved bifurcating tree and >2 for a node containing a polytomy.

From (3.1), we show analytically that a species with few preceding splits is taxonomically more distinct than one nested within a more diverse clade. However, because, as originally formulated, TD does not include information on branch lengths, it is highly sensitive to the resolution and the taxon sampling of the phylogeny. The addition of branch length information makes distinctiveness measures somewhat less sensitive to phylogenetic resolution and taxon sampling because estimates of time to shared ancestors are not strongly influenced by the exclusion of sister taxa, whereas the number of evolutionary splits is highly dependent upon the number of included species (3.1). Two recent derivations have expanded upon (3.1) to consider branch lengths in the calculation of distinctiveness. The first, Equal Splits (ES) (Redding and Mooers 2006; Redding et al. 2008), divides an edge length by the number of branches originating from the node directly below it (Fig. 3.1a). This formulation looks similar to TD but scales the number of splits at a node, v, by the length of the branch, λ_e, preceding it:

$$\text{ES}\ (T,i) = \sum_{e \in q(T,i,r)} \left(\lambda_e \prod_{v \in a(T,i,e)} \frac{1}{\deg_{\text{out}}(v)} \right). \tag{3.2}$$

The second, fair proportion or Evolutionary Distinctiveness (ED) (Isaac et al. 2007), is conceptually similar to ES but instead partitions edge lengths by the total

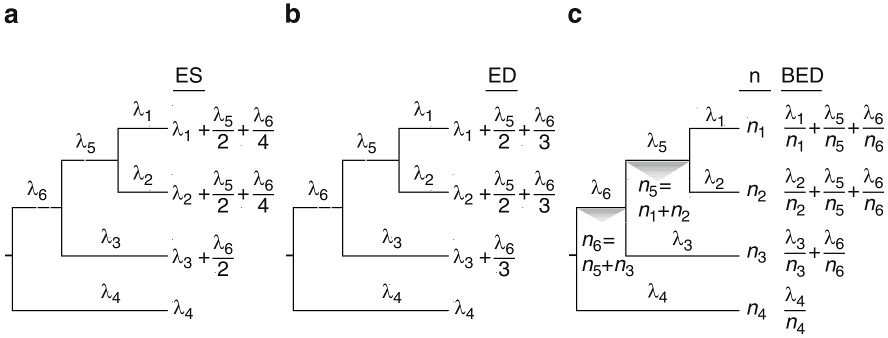


Fig. 3.1 Three methods of partitioning phylogenetic diversity (adapted from Cadotte and Davies 2010). (**a**) Equal Splits (Redding et al. 2008), ES, hierarchically partitions branch lengths by the number of descendent edges (line partitions on internal edges). (**b**) Evolutionary Distinctiveness (Isaac et al. 2007), ED, partitions branches by the total number of species descending from them. (**c**) Biogeographically weighted Evolutionary Distinctiveness (Cadotte and Davies 2010), BED, extends ED by partitioning PD by the numbers of populations or sites (n) associated with species descending from a node

number of species subtending it, not just the branches directly below it (see Fig. 3.1b) and is calculated as:

$$\mathrm{ED}(T,i) = \sum_{e \in q(T,i,r)} \left(\lambda_e \frac{1}{S_e} \right), \tag{3.3}$$

where e is a branch of length λ in the set $s(T,i,r)$ connecting species i to the root, r, and S_e is the number of species that descend from edge e. A nice feature of ES and ED is that they both independently sum to Faith's (1992) index of phylogenetic diversity (PD) – the sum of the phylogenetic branch lengths connecting species in a set (see Box 3.1).

3.3.4 Composite Metrics

Above, we have considered threat and evolutionary history separately, however, evolutionary history (PD) can be integrated with extinction probabilities for conservation prioritisation (e.g., Witting and Loeschcke 1995; Faith and Walker 1996; Weitzman 1998). More recently, both Redding and Mooers (2006) and Isaac et al. (2007) used extinction probabilities to weight the evolutionary distinctiveness measures ES and ED, respectively. For ES, Redding and Mooers (2006) quantify the Expected Loss (EL) of evolutionary history, as:

$$\mathrm{EL}_i = \mathrm{ES}_i \times \mathrm{Pe}_i, \tag{3.4}$$

where the ES of species i is multiplied by its probability of extinction, Pe.

Similarly, the weighted ED metric, which Isaac et al. (2007) refer to as EDGE (Evolutionarily Distinct and Globally Endangered), includes extinction risk, so that:

$$\mathrm{EDGE}_i = \ln(1 + \mathrm{ED}_i) + \mathrm{GE}_i \times \ln(2), \tag{3.5}$$

where GE values are taken from the IUCN Red List categories (http://www.iucnredlist.org). Thus, EDGE values are interpreted as the log-transformed expected loss of evolutionary diversity, where each increment in Red List ranking corresponds to a doubling of extinction probability (Isaac et al. 2007). Equations (3.4) and (3.5) are formulated identically, save a log-transformation, what differs is how they estimate extinction probability as well as the subtle difference in calculating evolutionary distinctiveness [equations (3.2) and (3.3)].

3.3.5 A Diversity of Metrics

To compare the relative performance of different biodiversity metrics, Davies and colleagues used the distribution of mammal species within ecoregions and a greedy complementarity algorithm, to maximise the capture of seven alternative biodiversity currencies (see Davies et al. 2008 for derivations):

- Species richness
- Expected extinctions
- EDGE
- EL
- Expected speciations (from recent diversifications)
- PD
- Latent risk

Reassuringly, there is broad agreement among most metrics (Fig. 3.2), likely because species-rich areas sum to higher values and, hence, rank highly across most currencies. Further, simulation studies suggest that some metrics might only diverge under a very narrow set of circumstances, for example, species richness and PD; (Rodrigues et al. 2005), although these conditions might be common

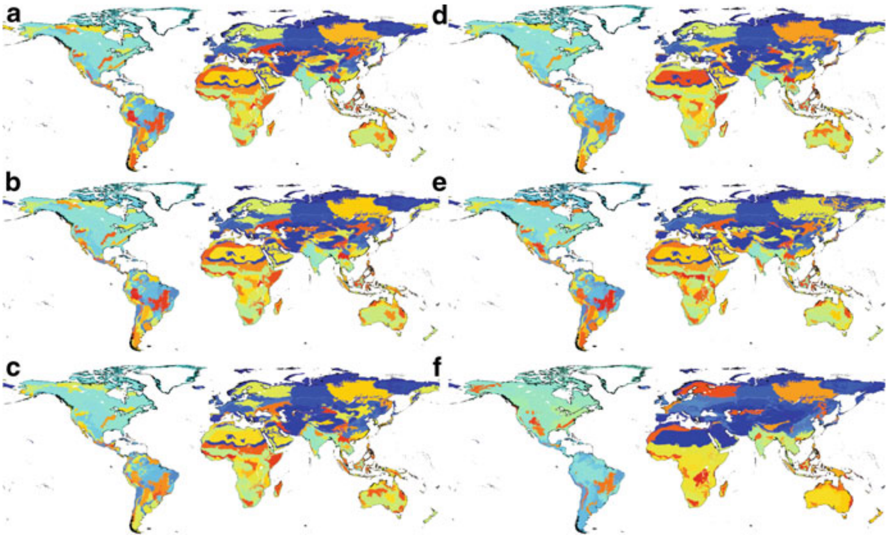


Fig. 3.2 Ecoregion complementarity rank under six different conservation currencies: (**a**) species richness, (**b**) EDGE, (**c**) EL, (**d**) species extinctions predicted in the next 100 years, (**e**) expected speciations, and (**d**) latent risk (the discrepancy between a species' current extinction risk and that predicted on the basis of its biological traits). The equivalent map for phylogenetic diversity (PD) is not shown, but matches closely that for species richness (Davies et al. 2008). Colours represent ecosystem ranking with red high rank and blue low rank

(Mace and Purvis 2008). Latent risk, which weights more highly species that are currently less threatened, most obviously departs from the general trend, unsurprisingly demonstrating the greatest disparity with expected extinctions – estimated from current threat. Choice of metric can, therefore, significantly alter prioritisation schemes and, even for metrics that appear largely congruent, there might be disagreement in the order in which regions are selected because the additional gains provided by the inclusion of each region into the priority set may vary considerably with conservation currency (e.g., Forest et al. 2007). Our comparison uses ecoregions as spatial units, which are at a larger scale than most conservation action plans. At finer spatial scales, it is likely that congruence amongst alternative conservation currencies will decrease (Grenyer et al. 2006), yet it remains unclear how this might influence complementarity rankings.

Improved algorithms and advances in computational processing speeds have allowed us to solve complex complementarity problems, considering multiple variables including costs (Margules and Pressey 2000; Sarkar et al. 2006). Increased availability of detailed data on species ecologies and geographies will continue to improve the accuracy with which rankings can be made. However, rankings will remain sensitive to the weightings we apply to alternative conservation currencies. At the extreme, we might assign weights equally across all species, by doing so we will of course capture alternative currencies as well, but suboptimally. Alternatively, we can weight species differentially, for example, using taxonomic distinctiveness or threat status, and include additional data on non-biological attributes, such as costs. Despite the rigour with which we can now address complementarity problems, solutions will, in part, reflect the subjective values we place upon the various aspects of biodiversity. In addition, because some currencies weight similar data very differently (e.g., current threat versus latent risk), global solutions that maximise all currencies are unlikely. Integrative metrics that simultaneously capture multiple attributes, for example, EDGE and EL, provide one way forward.

3.3.6 Integrating Space and Time

Global extinction risk and endemism provide useful indices of species' global vulnerabilities. However, within a defined geographical context, for example, political regions or a network of protected areas, a species' vulnerability is a product of its representation at these scales. Species with few populations or that occur only within a small subset of protected areas might warrant special attention. In addition, the evolutionary history encapsulated by a set of species will be differentially represented among sites (Rosauer et al. 2009; Cadotte and Davies 2010). Here we detail one approach developed by Cadotte and Davies (2010) that allows quantification of evolutionary distinctiveness within a species, multi-species sites or across larger multi-site regions. Cadotte and Davies refer to this metric as biogeographically weighted evolutionary distinctiveness (BED) and derive it as:

$$\mathrm{BED}(T,i) = \sum_{e \in q(T,i,r)} \frac{\lambda_e}{n_e}, \tag{3.6}$$

where n_e is the total number of populations or occupied sites that descend from branch e, with branch of length λ, in the set *q(T,i,r)* which includes the branches connecting species i to the root, r, of tree T (see "*BED*" Fig. 3.1c).

Cadotte and Davies introduce BED as an extension of a more general set of indices that add abundance information to measures of phylogenetic diversity (Cadotte et al. 2010). The sum of the species' BED values is again equal to total PD, meaning that the proportion of the total PD contained within single populations or sites can be calculated. Further, for species i, BED_i values can be used to evaluate species relative importance values, IV_i within and across sites:

$$\mathrm{IV}_i = \frac{\mathrm{BED}_i}{\sum_{i=1}^{S} \mathrm{BED}_i}. \tag{3.7}$$

IV_i values can be summed across species occurring at a single sampling site, reserve, or at larger spatial scales. High IV species have populations which are evolutionarily distinct relative to those for populations of other species. This metric assumes that the evolutionary divergences among populations within species have a length of zero, but this assumption can be modified (see Appendix 2 in Cadotte et al. 2010).

The total evolutionary distinctiveness represented by a single site t [as opposed to a single species – see (3.3)] with co-occurring species is:

$$\mathrm{ED}_t = \sum_{i=1}^{S} \mathrm{BED}_i. \tag{3.8}$$

Cadotte and Davies (2010) also provide a metric to calculate the conservation value, CV, of region L by summing the ED_t values across sites, standardised by the total number of sites sampled, N:

$$\mathrm{CV}_L = \sum_{t=1}^{N} \sum_{i=1}^{S} \frac{\left(\sum_{e \in q(T,i,r)} \frac{\lambda_e}{n_e} \right)}{N} \quad \text{or} \quad \mathrm{CV}_L = \frac{\left(\sum_{t=1}^{N} ED_t \right)}{N}. \tag{3.9}$$

This set of metrics allows researchers to consider the conservation values of species (IV), sites with multiple species (ED_t) and regions encompassing multiple sites (CV_L).

3.3.7 Non-Biological Metrics and Biodiversity Coldspots

Hotspots approaches, by definition, focus upon the goal of maximising the conservation of biodiversity, and we have considered here only currencies that attempt to capture directly biological or ecological variation. However, there are many additional conservation metrics that include subjective assessments based upon charisma or aesthetic and cultural values of species, etc. (Ehrlich and Ehrlich 1981). In addition, low-diversity ecosystems might still provide critical ecosystem services locally, such as clean water and fertile soils, as well as globally, such as climate regulation and clean air. Furthermore, the link between biodiversity and ecosystem services is non-linear (Kareiva and Marvier 2003); hence, impacts from the loss of diversity in species-rich systems might be relatively small, whereas gains from addition of diversity in species-poor systems might be large. Economic value can be placed upon these services (e.g., Balmford et al. 2002), and this can be incorporated into reserve selection algorithms, although true benefits might prove difficult to estimate (Turner et al. 2003), at least until after we lose the service provided.

Last, in this chapter, our focus has been on conservation benefits rather than costs. It is an unfortunate reality that conservation must be practised within a cost–benefit framework. Costs vary spatially by several orders of magnitude (James et al. 2001; Balmford et al. 2003), perhaps by more than the benefits of conservation do. Because threatened species tend to be concentrated in regions with high threat of habitat change and high human population density (Cardillo et al. 2004; Mace et al. 2005), returns per conservation dollar might be greatest from investing in intact but susceptible places, where conflicts are not yet entrenched (Balmford et al. 2003; Mittermeier et al. 2003; Cardillo et al. 2006). An optimal conservation network might then include both hotspots of endemism and rarity, as well as larger coldspots of inexpensive but low-diversity wilderness.

3.4 Conclusion and Future Challenges

Hotspots cannot provide a “silver-bullet” solution to the current biodiversity crisis because there is no single metric that can capture all aspects of diversity that we might value. However, it is urgent that we develop a common blueprint do address the global biodiversity crisis and stop duplicating efforts (Mace et al. 2000). Although conservation works at the margins and, as a consequence, prioritisation schemes can be sensitive to small differences, we might take some comfort from the knowledge that alternative schemes are themselves largely complementary. Many schemes identify the same or similar areas as conservation priorities (Brooks et al. 2006) – an obvious start would be to focus resources on these zones of overlap. However, cost effective conservation might also consider investing in currently healthy ecosystems that may become vulnerable in the future (Davies et al. 2008; Cardillo et al. 2006). If, as rational decision makers, we wish to maximise our conservation return on investment (Murdoch et al. 2007), low diversity "wilderness" might then prove sensible conservation investments (Mittermeier et al. 2003). We must also accept that some areas and some species represent bad investments. Efforts to prevent any further species extinctions (e.g., Alliance for Zero Extinction; http://www.zeroextinction.org/), although aspirational, are unfortunately fated to fail (Marris 2007; Mace and Baillie 2007). With a rapidly changing climate and growing human population, Vane-Wright's agony of choice has never been more acute.

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Chapter 4
Human Population and the Hotspots Revisited: A 2010 Assessment

John N. Williams

Abstract Using updated global population datasets from what was available in 2000, this chapter presents a revised assessment of human population numbers and growth rates in the biodiversity hotspots and tropical wilderness areas (TWAs). From 2000 to 2010, human population in the hotspots is projected to have increased by 187 million, to a total of almost 1.5 billion people. Human density in the hotspots in 2010 is estimated at 99 people per square kilometer, up 15% from 2000. While the TWAs are less densely populated than the hotspots, averaging 13 people per square kilometer in 2010, the human populations there are growing much faster: the annual growth rate averaged 3% per year – more than twice the rate for the hotspots. Despite the increases in absolute numbers and growth rates that are above the global average, the growth rates in both the hotspots and TWAs have declined over the last decade. The aggregate numbers are somewhat misleading, however, because the demographic patterns are heterogeneous from one region to another. This analysis examines both the inter- and intra-regional differences in population trends within the hotspots and TWAs, and concludes with a discussion of the relationship between population growth and development and how we as a species may influence these trends in the future.

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4.1 Introduction

In 2000, Myers and colleagues (2000) formally introduced the 25 biodiversity hotpots as the priority places across the globe where the highest levels of species richness, endemism and threat converged.[1] The authors proposed that the combination of diversity and threats merited a focused global conservation strategy to achieve the biggest gains given limited resources. In the 10 years since, the article has been cited more than 2,700 times in the scientific literature (ISI 2/24/10) with 506 citations in 2009 alone. Although it has its share of critics, and the number and extent of the hotspots themselves have been modified (see Williams et al. 2011), the concept has made an indelible mark on the way we think about, and set priorities for, biodiversity conservation.

At about the same time, Cincotta et al. (2000) presented a related analysis of human population in the hotspots, filling in an important part of the story about why the hotspots are threatened. The authors calculated that as of 1995, the 25 hotspots, while making up 13% of the Earth's inhabitable surface, were home to 1.1 billion people, or 19% of its human population. Equally important were the statistics on growth: the authors estimated that the global human population growth rate from 1995 to 2000 was 1.3%, while the rate in the hotspots for the same period was 1.8%, or 38% higher. Thus, not only were the hotspots home to almost one fifth of the world's population, but they were also becoming more crowded and growing more rapidly than the rest of the world. Because the threats to biodiversity in the hotspots are primarily human-related, this analysis suggested that biodiversity would be increasingly threatened by local population growth.

In the past decade, population in the hotspots continued to grow faster than the global average – there are now almost 1.5 billion people, or 21% of the human population, living in these priority conservation areas. This chapter assesses how human demography in the hotspots has changed from 2000 to 2010. It comes on the eve of the world's population hitting seven billion people, just as the previous analysis appeared shortly after the six billion mark.

This update takes a revised look at the population numbers and trends specifically in the hotspots and tropical wilderness areas (TWAs), examining the growth rates and details that will determine what happens in the next 10 years and beyond. It also highlights the aspects of the demographics that require the most urgent attention, both in terms of conservation and human well-being. The analysis reveals that while many of the changes in the last decade reflect what was anticipated, there are also some alarming changes, as well as some reasons for renewed optimism.

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[1] Myers first introduced the hotspot concept in an earlier paper highlighting ten priority areas (Myers 1988).

4.2 Methods

For consistency and comparability, the primary analysis conducted here used the same 25 hotspots and TWA delineations used by Cincotta et al. (2000). All spatial analyses were conducted in ArcGIS (ESRI 2005). Additional analyses were conducted on a revised set of hotspot delineations (Mittermeier et al. 2005) available online (http://www.conservation.org/explore/priority_areas/hotspots). Because most of the revised hotspots represent refinements of the initial priority areas, this report focuses on the original designations. Attention is given, however, to demographic trends occurring in the areas that represent entirely new priority areas or major changes in the original designations.

The primary source of population data used is the raster dataset from the Gridded Population of the World, version 3 (CIESIN 2005). Estimates for 2010 and 2015 represent projections made by CIESIN based on recent trends. Calculations for the individual hotspots were made by overlaying the hotspot boundary on the population raster and calculating the sum of the grid cells contained therein for population, and the mean value of the grid cells for density using the zonal statistics function in the spatial analyst toolkit. Population and density estimates for the hotspots and TWAs are also given for 2008, which were calculated in the same manner using a separate independent dataset (ORNL 2009). The 2008 estimates are shown to provide support for the CIESIN data and to highlight the level of uncertainty surrounding some of the numbers. Additional estimates for population totals and growth by country and region come from the 2008 update of the United Nations Population Division and the International Database of the United States Census Bureau.

4.3 Aggregate Numbers: Then and Now

At the time of the Cincotta et al. (2000) analysis, the population numbers for the 2000 round of national censuses were still coming in. With the benefit of hindsight, this analysis of the 2000 data reveals that the rate of growth in the hotspots was not as high as the authors estimated. This analysis found growth in the hotspots during the period 1995–2000 to be 1.6% instead of 1.8%. The revised number is still significantly higher than the world as a whole, whose growth during that period has been revised upward to 1.4% (UN 2008b). Population in the TWAs also appears to have grown more slowly than the authors estimated – 2.8% instead of the 3.1% estimated for the same period.

Despite these revisions, the numbers still indicate that the absolute number of people living in the hotspots and TWAs increased at a rate faster than the global average. Put in terms of population size, from 1995 to 2000 cumulative growth in the hotspots and TWAs was approximately 107 million people – a large number considering that the livelihood and resource demands for most of those people likely came from within the respective hotspots or TWAs.

In the decade since 2000, there is reason for both optimism and concern with respect to human population trends in the hotspots and TWAs. In all except the California Floristic Province, the Polynesia-Micronesia hotspot and the Congo TWA, the rate of population growth has decreased. In aggregate terms, total population growth in the hotspots slowed from 1.6% during the 1995–2000 period to a projected 1.3% during the 2005–2010 period. By comparison, world annual population growth rate slowed from 1.4 to 1.2%. Projections to 2015 suggest that these slowing trends are expected to continue.

While the decreasing rates offer hope for demographic transition, the absolute population numbers are still cause for concern (Table 4.1). Only one hotspot, the Succulent Karoo of South Africa and southwestern Namibia, has experienced a net decrease in the human population in the past decade – a reduction that is probably due more to economic decline and the resulting rural-to-urban migration than reduction in fertility rates (Nel and Hill 2008, Reyers et al. 2009). From 2000 to 2010, the population of every other hotspot increased by an average of more than 7%, for a total population increase across the hotspots of 187 million people.

Although related to total population numbers, population density gives important additional information about how people are distributed across the landscape and where the human activities that have the most impact on biodiversity – such as land conversion, deforestation, harvesting and exploitation of threatened species – may be most intense. Figure 4.1a shows a map of human density for the hotpots and TWAs, while Fig. 4.1b shows how density has changed across the globe in the last 10 years. It is clear from these two maps that compared to the rest of the world, population densities within the hotspots and TWAs are both high and getting higher.

Human population dynamics in the TWAs tell a mixed story (Fig. 4.2). In absolute terms, the TWAs have fared better than the hotspots because they had lower densities of people to start with – about nine people per square kilometer in 2000 compared to 87 people per square kilometer in the hotspots at the time. In 2010, that number is projected to be almost 13 people per square kilometer. Cumulatively, population in the TWAs increased by 30 million people, or 34%, from 2000 to 2010. The annual population growth rate of 3% during that time is equivalent to a doubling time of roughly 23 years. That represents an increase over the previous decade, although the average growth rate for the TWAs would have declined if not for the influence of the Congo.

The comparatively high growth rates in the large and sparsely populated TWAs are not entirely unexpected. Rural populations generally have higher fertility rates than their urban counterparts, as well as decreased access to markets, education, health services, family planning and other government resources and infrastructure (de Sherbinin et al. 2008). The more remote an area and the fewer people that live there, the harder and more expensive it is for governments and other organizations to extend such services to those people. Partly because of this remoteness and partly out of habit or custom, people living in these areas depend heavily on natural

Table 4.1 Population growth and density in the biodiversity hotspots and tropical wilderness areas (TWAs) from 2000 to 2010. Numbers from 2008 in bold represent > 10% disparity from 2010 estimate

Hotspots/Tropical wilderness areas	Population (in thousands)			Growth %$^{-\text{Yr}}$	Density km^{-2}
	2000[a]	2008[b]	2010[a]	2000–2010	2010[a]
Succulent Karoo	289	**313**	269	-0.7	1.4
Caucasus	16,694	15,699	16,859	0.1	94.1
Cape Floristic Province	4,021	**4,830**	4,221	0.5	54.3
New Zealand	3,223	3,710	3,416	0.6	14.8
Mountains of Southwest China	12,055	13,062	12,895	0.7	28.5
Western Ghats & Sri Lanka	46,504	45,964	50,173	0.8	371.2
Mediterranean Basin	187,442	211,635	206,655	1.0	141.0
Caribbean Islands	43,265	46,565	47,942	1.0	173.7
Chilean Forests	13,319	15,532	14,928	1.1	45.8
Southwest Australia	1,545	1,754	1,735	1.2	18.4
Sundaland	212,398	238,244	238,677	1.2	167.6
Atlantic Forests	81,511	95,909	91,708	1.2	115.2
Wallacea	25,937	29,289	29,321	1.2	95.0
Polynesia–Micronesia	3,155	3,529	3,630	1.4	94.0
Indo-Burma	241,139	261,604	277,813	1.4	123.6
Tropical Andes	70,954	75,228	82,324	1.5	57.9
Brazilian Cerrado	12,012	13,515	14,013	1.6	6.5
Choco-Darien-Western Ecuador	6,062	**5,570**	7,158	1.7	56.2
California Floristic Province	33,125	35,666	39,151	1.7	164.1
Philippines	74,696	94,854	88,568	1.7	317.8
Mesoamerica	66,415	74,906	78,842	1.7	72.6
New Caledonia	193	**203**	232	1.9	17.9
Eastern Arc Mountains	9,876	12,005	12,233	2.2	81.4
Guinean Forests of West Africa	81,365	102,644	105,474	2.6	165.6
Madagascar and Indian Ocean Islands	18,614	22,887	24,226	2.7	43.0
Hotspot Total/Average	*1,265,809*	*1,425,116*	*1,452,464*	*1.4*	*99.5*
TWA-Amazonia and Guiana Shield	18,330	21,092	23,175	2.4	4.1
TWA-New Guinea and Melanesian Islands	7,899	9,463	10,032	2.4	11.8
TWA-Congo Basin	62,661	82,640	85,693	3.2	30.1
TWA Total/Average	*88,891*	*113,195*	*118,900*	*3.0*	*12.6*
World – medium variant[c]	6,115,367	6,750,062	6,908,688	1.2	51

Estimates calculated using priority area polygons from Cincotta et al. (2000) and the Gridded Population of the World, v. 3 for 2000 and 2010 (CIESIN 2005), and from Landscan for 2008 (ORNL 2008). Numbers from 2010 are projected

[a] CIESIN (2005)

[b] ORNL (2009)

[c] UN (2008b)

resource extraction to meet their daily needs (Barbier 1997; Bahuguna 2000), even if those resources are inside a protected area (Fiallo and Jacobson 1995; Jha and Bawa 2006). This combination of limited economic alternatives, population growth

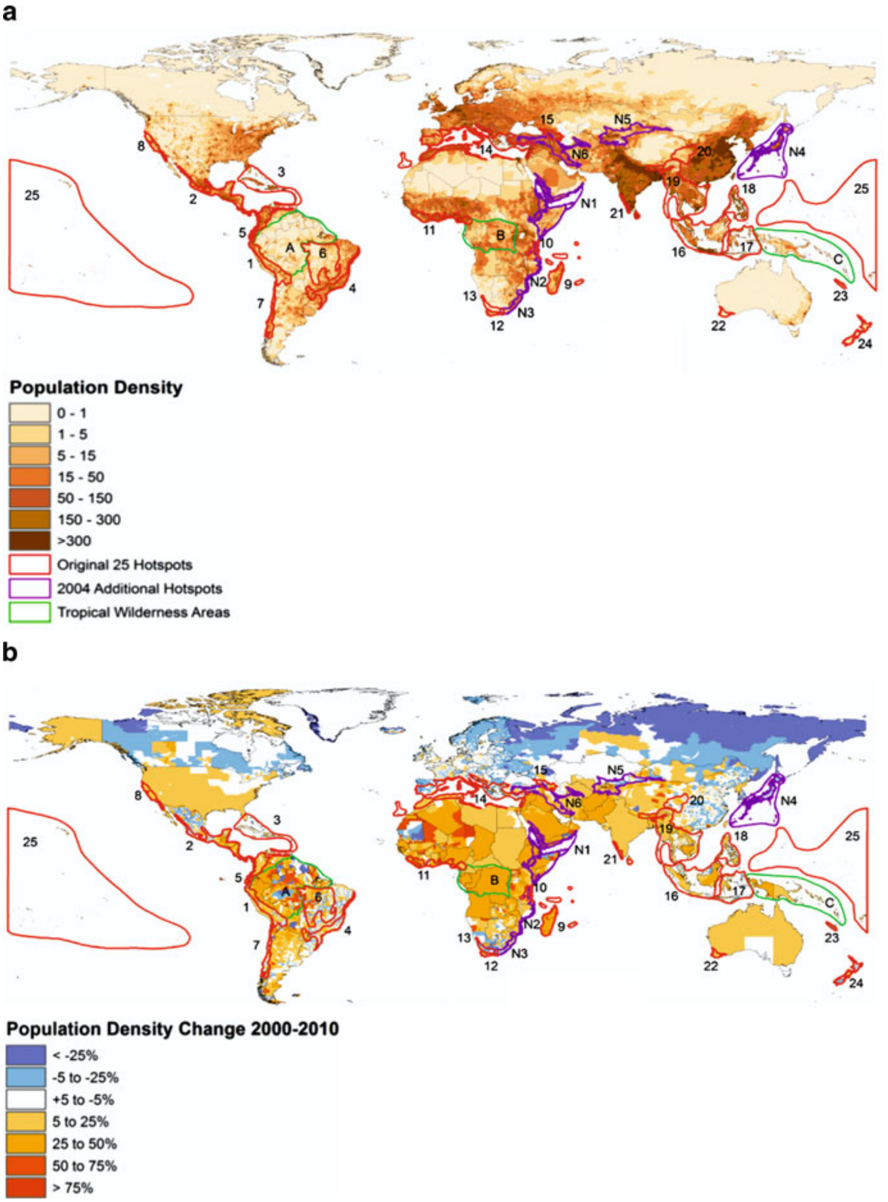


Fig. 4.1 Population density (**a**) and density change (**b**) in the biodiversity hotspots and major tropical wilderness areas from 2000 to 2010. Priority area polygons based on Cincotta et al. (2000) and Mittermeier et al. (2005). Density based on people per square kilometer for smallest available administrative unit as mapped by the Gridded Population of the World, v.3 (CIESIN 2005). The original 25 hotspots are: (1) Tropical Andes; (2) Mesoamerica; (3) Caribbean Islands; (4) Atlantic Forests; (5) Choco-Darien-Western Ecuador; (6) Brazilian Cerrado; (7) Chilean Forests; (8) California Floristic Province; (9) Madagascar and Indian Ocean Islands; (10) Eastern Arc Mountains; (11) Guinean Forests of West Africa; (12) Cape Floristic Province; (13) Succulent

and isolation suggests that stabilizing the human footprint in these areas may be a slower process than in other more densely populated but less remote hotspots.

4.4 Regional Trends

4.4.1 Indo-Pacific

One of the prominent characteristics of the hotspots is the importance of island assemblages and archipelagos. Eight of the 25 hotspots fall into this category. That the island hotspots harbor unusually rich levels of species diversity and endemism is not surprising. More than 150 years ago, when Charles Darwin and Alfred Russell Wallace were developing their theories of evolution, they recognized the uniqueness of island biotas and how isolation related to speciation. As more recent research indicates (Paulay 1994; Fordham and Brook 2010), many of the same characteristics that make islands crucibles of speciation – including open niche space, ecologically naïve species, isolation and restricted geographic ranges – also make them unusually vulnerable to extinctions.

Many of the threats facing island biota come directly from human pressures (though see Denslow (2003) for a discussion of the role of introduced species). Nowhere do biodiversity and high human population densities come face-to-face more acutely than in the Indo-Pacific biogeographic region, which contains multiple island hotspots and the New Guinea and Melanesia TWA. The region extends from the western islands of the Indian Ocean to the eastern edge of Oceania (Spalding et al. 2007). Population density and high growth rates are well above global averages throughout this region. The Western Ghats and Sri Lanka hotspot has the highest population density of any hotspot, and not surprisingly has high related rates of deforestation and degradation induced by such pressure (Shi et al. 2005; Joseph et al. 2009). The Philippines hotspot has increased by almost 14 million people in the last decade, and ranks second in terms of population density. These factors, combined with moderate levels of poverty (2009 per capita GDP of \$3300, 33% below poverty line, (World Bank 2009)), make the Philippines among the most at-risk hotspots. With both demographic and economic pressures driving the extensive conversion of forests and overexploitation of coastal resources (Shi et al. 2005; Fisher and Christopher 2007), the Philippines has suffered such

Fig. 4.1 (continued) Karoo; (14) Mediterranean Basin; (15) Caucasus; (16) Sundaland; (17) Wallacea; (18) Philippines; (19) Indo-Burma; (20) Mountains of Southwest China; (21) Western Ghats and Sri Lanka; (22) Southwest Australia; (23) New Caledonia; (24) New Zealand; (25) Polynesia-Micronesia. A subset of the hotspots added in the 2005 revision include: (N1) Horn of Africa; (N2) Coastal Forests of Eastern Africa; (N3) Maputaland-Pondoland-Albany; (N4) Japan; (N5) Mountains of Central Asia; and (N6) Irano-Anatolian. The tropical wilderness areas are: (A) Amazon and Guiana Shield; (B) Congo Basin; and (C) New Guinea and Melanesian Islands

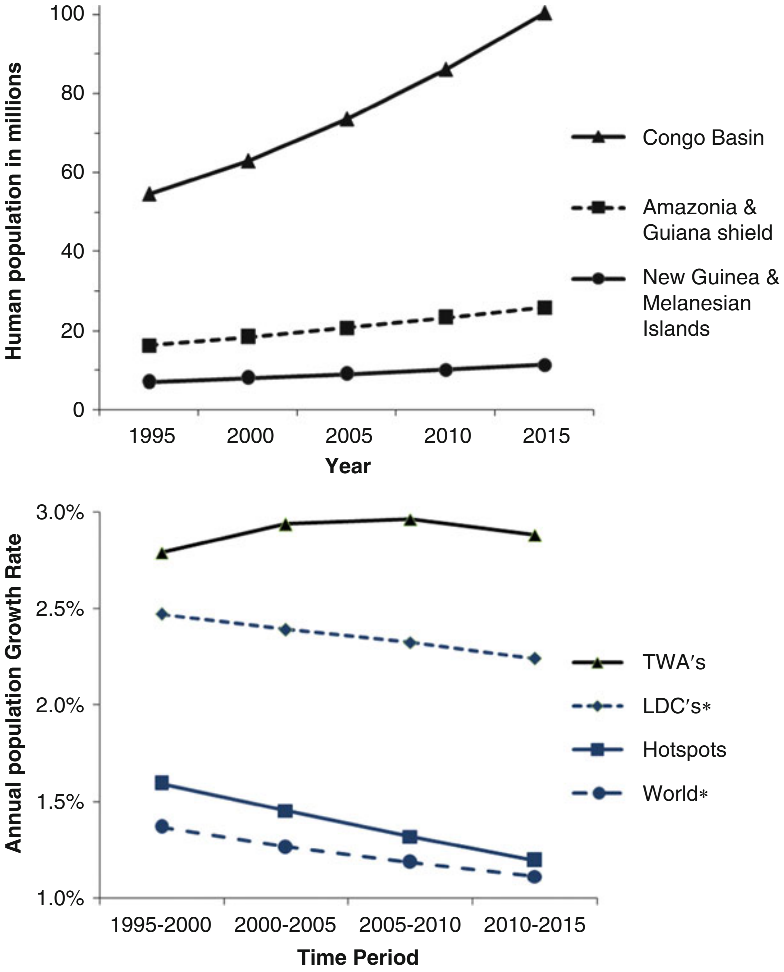


Fig. 4.2 Population Growth in the Tropical Wilderness Areas (TWA's) from 1995 to 2015. The upper figure shows the population growth in the three major TWA's in absolute terms, while the bottom figure shows the average annual growth rate (by area) in the TWA's relative to the average for the least developed countries (LDC's – 49 countries: 33 in Africa; 10 in Asia; 5 in Oceania; plus one in Latin America and the Caribbean), the 25 original hotspots and the world. Numbers for 2010 and 2015 are projected. *Numbers for LDC's and world are from the United Nations Population Division 2008 Update, medium variant

widespread degradation of terrestrial and marine resources that a debate has ensued about whether its diversity is beyond salvage (Terborgh 1999; Posa et al. 2008).

Elsewhere in the Indo-Pacific, population growth is associated with habitat degradation and increased exploitation of both the terrestrial and marine biodiversity (Roberts et al. 2002; Sodhi and Brook 2006). The Wallacea and Sundaland hotspots, which fall mostly within the national boundaries of Indonesia, have two and three times the average global population density, respectively. Such densities are not anomalous for Indonesia, however, which is the fourth most populous country in the world, and has a median age of 27.6 years and TFR (Total Fertility Rate) equal to 2.6 children per woman. By comparison, the United States has a median age of 36.7 years and a TFR of 2.1 (UN 2008a).

These statistics suggest that population momentum will continue to add to Indonesia's population even as fertility rates drop (see Box 4.1). Furthermore, almost 50% of the Indonesian population lives in rural areas (UN 2007) – a feature of the country's demography that does not bode well for conservation. Fortunately, socio-economic indicators for Indonesia (2009 per capita GDP of $4000, 18% below the poverty line, human development index (HDI) of 0.734 (UNDP 2009, World Bank 2009)) suggest that the country is considerably better off than much of the developing world and may avoid some of the biodiversity loss associated with extreme indicators of poverty (Fisher and Christopher 2007).

By contrast, Madagascar and the Indian Ocean islands is one of the poorest and fastest growing of the hotspots. With 50% of Madagascar's population below the poverty line and an HDI of 0.543, the country has grown by five million people, or 32%, since 2000. It also has a high TFR of 4.8 children per woman (UN 2008a), a low rate of urbanization of 29% (UN 2007), and a young population with a median age of 18 years – all of which are linked to the high rates of deforestation on the island (Brooks et al. 2009a, Whitehurst et al. 2009). The relatively low population density of the hotspot is the one demographic measure that offers some hope that there is time to enact changes. That change needs to occur soon, however, because if the population profile present in 2010 continues – i.e., young, poor and largely rural – forest conversion will continue and irreversible loss of biodiversity is likely to occur.

Demographically, the Indo-Burma hotspot can be characterized by high population densities. Culturally and economically, it is a heterogeneous region. The economic growth and urbanization that are rapidly changing the socio-economic profiles of countries like Malaysia and Thailand, for example, are largely absent in countries like Burma and Laos. High population density combined with high growth rates affect biodiversity in different ways throughout this hotspot, but an unfortunate and unifying result is some of the highest rates of forest loss anywhere in the tropics. This region is also at risk of high numbers of species extinctions – a situation that is exacerbated by a thriving illegal species trade and widespread government corruption (Sodhi et al. 2010).

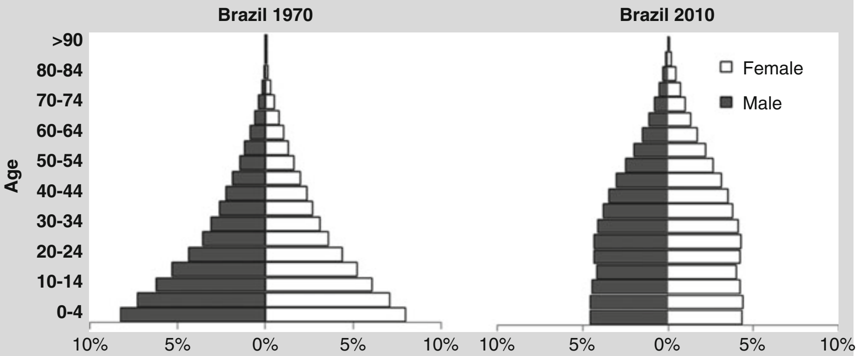
4.4.2 Africa

Just as Africa is ecologically and culturally diverse, the ways in which population trends relate to biodiversity on this continent are also complex. A striking example is in the southern tip of Africa, where two unique hotspots border one another. The Succulent Karoo has the lowest population density of any hotspot (1.4 people per square kilometer), and is the only one with negative population growth (according

Box 4.1. Total Fertility Rate and Population Momentum

The total fertility rate (TFR) is the average number of children a woman would bear over the course of her lifetime if current age-specific fertility rates remained constant throughout her childbearing years (ages 15–49). The current TFR is usually taken as an indication of the number of children women are having at the present, and is calculated from the fertility data of all age cohorts in the population (UN Population Division definition). As TFRs drop due to changes in attitudes about the desired number of children to have, or to increased access to reproductive health and family planning services, the *rate* of growth will begin to slow. However, population growth itself will not slow until women entering their reproductive years collectively have fewer children than older cohorts of women had (or unless mortality rates increase).

This concept is illustrated well by the case of the megadiversity country of Brazil, which contains much of the Atlantic Forest hotspot and the Amazon tropical wilderness area. From 1965 to 1970, the TFR for Brazil was 5.4 children per woman. That number has dropped steadily since, to the point where, from 2005 to 2010, it was at 1.9, or below replacement (UN 2008a). Yet Brazil's population continues to grow, and will until the broad base on the population pyramid to the left, below, makes its way through the reproductive years. Much of this transition has already occurred, as seen in the figure on the right, but the cohorts will continue to even out into upper age classes and, if TFR remains below replacement, the lower age classes will become smaller than those above them. This kind of transition in age structure is typical of countries moving from a state of lesser economic development to one of greater economic development. It is also associated with greater economic and political stability as well as improved human and environmental health (Leahy et al. 2007). Many of the important hotspot countries in Latin America and Southeast Asia have experienced population changes similar to Brazil, while many in Sub-Saharan Africa have profiles that are closer to that of Brazil in 1970.



Population pyramid data source: US Census Bureau, Population Division, International Data Base, 2010.

to the CIESIN data; the ORNL data show a slight increase since 2000). Adjacent to it, the Cape Floristic Province has roughly 40 times that population density. Although the annual population growth rate in the Cape hotspot is positive, it is relatively low (0.49%), making the overall population size fairly stable. While both areas are of critical conservation concern, agriculture, urban expansion and invasive species – more than human population growth – make up the major threats facing biodiversity in these hotspots (Mittermeier et al. 2005; Shi et al. 2005).

By contrast, the other hotspots in Sub-Saharan Africa are all experiencing rapid population growth. The Guinean Forests hotspot, with a growth rate twice the global average, has grown by more than 24 million people in the last decade. This is also one of several African hotspots where biodiversity is threatened by civil unrest. Especially in West Africa, armed conflict is frequently coincidental with population pressure in areas of high biodiversity, including parts of Nigeria (the most populous country in Africa), Sierra Leone, Liberia and Ivory Coast (McNeely 2003; Hanson et al. 2009).

The Eastern Arc Mountains hotspot, with a density of 80 people per square kilometer, has grown by 24% since 2000. The revised and expanded version of this hotspot, now called the Eastern Afromontane hotspot, has considerably higher population density (over 120 people per square kilometer) due to the inclusion of parts of the Albertine Rift Mountains to the north and the Rift Valley to the south. It also has an extensive history of political conflict threatening many imperiled species. Although not steeped in conflict, the more recently designated Coastal Forests of Eastern Africa and the Maputaland-Pondoland-Albany hotspots have similar population densities. Both hotspots face high rates of deforestation and habitat degradation that contribute to their critical conservation status (Burgess et al. 2006).

The high human densities and poverty endemic to central and eastern Africa mean that many conservation areas are experiencing the types of resource use and exploitation associated with rural areas, but on a scale commensurate with urban densities. Especially in areas of civil unrest, the line is blurring between rural areas and small urban centers, where both are driving demand for the exploitation of biodiversity (East et al. 2005; Mwampamba 2007). For example, in the markets of Goma, Democratic Republic of Congo (DRC), a city of more than 600,000 people, there are informal but well-established bushmeat and charcoal trades supplied by illegal extraction from neighboring Virunga National Park (R. Williams, Virunga Fund, personal communication).

There is a positive correlation between human population density and species diversity in sub-Saharan Africa that is both historically interesting and alarming. The coincidence of dense human settlements together with high concentrations of vertebrate species in the African Rift Valley, for example, suggests similarities in the conditions that were attractive for people and animals – namely a benign climate with an ample food supply (Fjeldsa and Burgess 2008). The numbers and resource demands of the human population in 2010, however, put pressures on the biodiversity that are without historical precedent. In particular, these areas are characterized by a young demographic with high fertility rates living in conditions of poverty and political instability – conditions that promote exploitation and overharvesting of wildlife and forests (Burgess et al. 2007; Cordeiro et al. 2007).

Perhaps more than any other priority area, the Congo Basin TWA illustrates how the nexus of population growth, poverty and civil unrest negatively impacts biodiversity (de Merode et al. 2004, 2007). Although the Congo TWA had a population density of only 30 people per square kilometer in 2010, that figure is deceptive because it is aggregated across a huge area, hiding the contribution of certain high density areas. As an illustration of this point, the provinces of eastern DRC have densities twice the TWA average (based on unofficial estimates for individual provinces found at http://en.wikipedia.org/wiki/Democratic_Republic_of_the_Congo). A critical anchor for African biodiversity, the DRC is a megadiversity country (Mittermeier et al. 1997) that has been in nearly constant civil conflict at least since 1997, when its authoritarian leader, Mobuto Sese Seko, was ousted. While the TFR fell by 14% in the last decade to 6.1 children per woman (a faster decline than Africa as a whole, which decreased 12% in the same period to 4.6 children per woman), it still remains exceptionally high. The high TFR, in combination with a median age of only 16 years, 67% of the population living in rural areas, and weak-to-non-existent government infrastructure in much of the central and eastern parts of the country, means that the DRC will be slow to reduce its population growth (UN 2007, 2008a). In addition to the demographic situation, the DRC is ranked last by the World Bank in terms of per capita GDP (less than $1 per day) and 176th out of 182 countries with data for the HDI. This level of extreme poverty is likely to continue to drive a desperate population to depend heavily on natural resources, including bushmeat, for both personal consumption and added income (de Merode and Cowlishaw 2006).

4.4.3 Latin America and the Caribbean

Of the three main continental regions examined here, Latin America and the Caribbean (LAC) has the lowest average human population density and rate of population growth within the conservation priority areas considered. Much of the LAC went through a demographic transition from the mid-1960s to the mid-1990s that brought average TFR down by 50% to a regional average of three children per woman (UN 2008a). The age structure of the region also transitioned to an older population during that period. Although historical data are incomplete for most countries, a look at Brazil, the most populous country in the region, is illustrative of the general pattern. In 1970, the median age in Brazil was 18, and 43% of the population was age 14 or younger. These numbers contrast with 2010, where the median age is 29 and only 26% are age 14 or younger (see Box 4.1).

Other factors that affect how populations impact biodiversity have also changed in the LAC region. Over the last 40 years, a steady trend of urbanization has resulted in a population that is now more than 78% urban (UN 2007). Economic conditions have also improved during that time: from 1969 to 2009, real per capita

GDP for the region increased by 389% (World Bank 2009). Finally, civil unrest, which was a major destabilizing force in much of the region from the end of the Cold War era through the 1980s, has decreased dramatically in the last 20 years. It is important to note, however, that in the course of LAC's economic and demographic transitions, the benefits have not been felt evenly across the landscape (Korzeniewicz and Smith 2000). In addition to a lack of improvements for parts of the human population, some environmental threats have become more serious as a result of the transitions that occurred, including increased per capita energy and natural resource consumption associated with improvements in living standards (for a more thorough analysis see Meyerson et al. (2007), Kramer et al. (2009), and Rudel et al. (2009)).

Greater population stability and economic improvements notwithstanding, demography still plays a role in some of the threats facing priority conservation areas of the LAC region. In the Caribbean Islands, which ranks third highest among all hotspots in population density, 38–45% of the remaining vegetation cover is at risk from population pressure (defined as densities above 100 people per square kilometer by Shi et al. (2005)). In the Mesoamerican hotspot, which has increased by 12 million people, or 19%, since 2000, both forest cover and vertebrate population declines have been associated with high human population density (Miles et al. 2006; Vazquez and Gaston 2006). The Atlantic Forest hotspot, with less than 10% of its original vegetation remaining, has also increased by ten million people during the past decade. Finally, the Amazon TWA, while less densely populated than other LAC hotspots, is nevertheless experiencing deforestation associated with high population densities (Armenteras et al. 2006; Dutra Aguiar et al. 2007). At current annual growth rates, the human population in the Amazon is expected to double in less than 30 years.

A sizable fraction of the human population growth in the LAC priority areas has occurred in lowland tropical forests, where deforestation has been associated with colonization of forest lands by frontier settlers (Carr 2008; Carr et al. 2009). Studies also indicate that high fertility rates among rural frontier populations and indigenous populations of the lowland tropical forests are far higher than national or rural averages (McSweeney and Arps 2005; Bremner et al. 2009; Carr et al. 2009). The LAC rural areas that are also home to hotspots are, like their Asian and African counterparts, typically underserved in terms of access to basic health services, including reproductive health services (see Box 4.2). Lack of these basic services has been positively linked to higher relative population growth rates, lower health quality metrics, increased poverty and habitat degradation (Cincotta and Engelman 2000; Margoluis et al. 2001; Engelman et al. 2006; Steele et al. 2006; Nash and De Souza 2007).

4.4.4 Other Hotspots

Of the hotspots not discussed above, the California Floristic Province is most notable in terms of its population dynamics. It has the highest population density

Box 4.2. Population, Health and the Environment

This chapter is about how and where the human population is threatening the areas of the highest biodiversity around the globe. One of the recurrent themes is how population growth in poor, rural areas leads to loss of species and habitats. At least part of the implied solution is that growth rates in these areas need to decrease or become negative if biodiversity is to be saved. That is true, but it would be an error to interpret this solution to mean that fertility or population growth rates are to be imposed on populations. Such an approach could be considered authoritarian, imperialistic, even genocidal in nature, as well as a violation of individual freedom and civil rights.

Remarkably and fortunately, the solution lies in increasing people's rights and freedom. It has been shown repeatedly and in numerous countries, that when boys and girls get equal access to education and when rural men and women get improved access to healthcare, including reproductive health services and family planning, families get healthier, less poor and fertility rates drop (UNFPA 2005). The data suggest that when land and resources are limited, and people know that they and their children will survive, they choose to have smaller, healthier families. That is good news from a conservation perspective, but even better news for the people living in these communities, whose access to these services comes with drops in maternal, child and infant mortality, decreases in HIV/AIDS, reductions in teen pregnancy and abortions and overall improvements in standards of living (UNFPA 2004; PAI 2006).

Not only do the links between access to basic health services and decreased fertility rates benefit conservation on the macro-scale of entire hotspots, but they also help ensure environmental sustainability on the level of the individual communities where the beneficiaries of these services live. Evidence from integrated population, health and environment projects undertaken by governments and non-governmental organizations alike has found that in rural communities where people have smaller families and improved health, they make decisions about land and natural resource use that are based on longer time horizons and result in greater sustainability of those resources (Margoluis et al. 2001; USAID 2005; Steele et al. 2006; Nash and De Souza 2007; PRB 2007). It makes sense: if people who depend on their environment for their livelihoods are healthy, and they know that they and their children are likely to remain healthy, they are going to take care of the place where they live.

of the hotspots located within developed countries (UNDP 2009), and it is the only hotspot whose annual population growth rate increased over the previous 5-year period. Unlike many of the other hotspots experiencing population growth, however, much of the increase in California comes from migration. From 2000 to 2008, international immigration was responsible for 42% of the population increase (before considering net domestic emigration) – a number that remains unchanged from the previous decade (USCB 2008). California also differs from many of the other hotspots in that much of the population-related threats to biodiversity are manifested through urbanization and related development (Lawson et al. 2008; McDonald et al. 2008, 2010).

Population trends for the Mountains of Southwest China hotspot are somewhat ambiguous. As drawn in the original hotspots map, the area has a relatively low population density and slow natural growth. As redrawn for the revised hotspots, however, the area borders on several urban areas, including Chengdu, a city of 11 million people and a major economic hub. The natural- and migration-related growth of Chengdu and other urban centers, including those associated with the Three Gorges Dam, may spill over to affect this hotspot and skew its demographics substantially.

The Mediterranean Basin is a densely settled hotspot with a long history of human presence. As such, it continues to experience habitat fragmentation, forest conversion, urbanization and development-related degradation of natural resources (Coll et al. 2008; Palahi et al. 2008; Underwood et al. 2009). While the annual growth rate, at 1%, is low as a regional average, the hotspot is demographically heterogeneous. Among the 27 countries contained by the hotspot, growth rates vary from negative population growth in Slovenia to more than 3% annual growth in Jordan. Population growth rates are the highest in the eastern and southern parts of the basin, particularly among the Middle Eastern and North African countries, although parts of coastal Spain are also experiencing increasing growth rates. Elsewhere in the hotspot, including in the northwest, urbanization and related development threaten remaining fragments of natural habitat (McDonald et al. 2008). Overall, Shi et al. (2005) estimated that 37% of closed forests in the hotspot were vulnerable to population pressures and 25% of the other natural vegetation types were also at risk. Those estimates have likely increased since that study was conducted, given that the average population density in the region is projected to have increased from 2005 to 2010.

The analysis conducted here was guided by querying geospatial data aggregated across many countries and regions. Errors of commission and omission are likely included. Commission refers to mistakes made by the author in interpreting the results, as well as mistakes made by others along the way who had the difficult task of converting and combining disparate datasets of varying formats. Omission refers to important aspects of how human population affects biodiversity that were either not presented or not visible at the resolution of this study. The New Zealand, Western Australia and Caucasus hotspots, for example, were not mentioned as being affected by population pressures because, while their biodiversity is threatened, those threats are not generally perceived to be directly related to high human densities or rapid population growth. This is not to say that nowhere in these hotspots does human population affect biodiversity. Rather, it is to suggest that from the global perspective taken here, the impact of human population growth in these places is small relative to other threats and relative to other hotspots.

4.5 Conclusions and Discussion

This chapter has presented an update on how human population in the hotspots and major tropical wilderness areas has changed from 2000 to 2010. Across the hotspots, the data show that the annual population growth rate has declined, although it is still above the global average. Despite the slowdown in growth, population in the hotspots and TWAs is projected to have increased by more than 200 million people since 2000. While less densely populated, the TWAs have experienced growth rates more than twice the average for the hotspots. Aggregate numbers such as these can be misleading, however. Population growth has varied from a net loss of people in the Succulent Karoo to an increase of more than 30% for Madagascar and the Indian Ocean Islands. Likewise, population density in the hotspots today varies from just over 1 person per square kilometer to more than 370 people per square kilometer. Such variation notwithstanding, it is possible to generalize that human population growth has been most acute in sub-Saharan Africa, followed by south-central Asia, southeastern Asia and Oceania, and then by Latin America and the Caribbean.

While slower growth rates compared to 10 years ago reflect reductions in fertility rates and aging population structures (UN 2008a; USCB 2010), the populations, especially in most of the developing world hotspots, are still largely characterized by cohorts that have either yet to enter their reproductive years or are in the early stages therein. This combination suggests that momentum will augment human population in these priority conservation areas, even as growth rates continue to fall.

Much of the impact that we as a species have on our local environment can be captured by a straightforward formula: the number of people multiplied by the impact per person. While this equation ignores a number of important complexities – including global warming, the impacts of war, and pollution from point sources like factories or industrial accidents – those, too, can be averaged across the population. The result is that in order to reduce our impact, we either have to decrease our numbers, our individual impacts, or better yet, both. This chapter has left alone the discussion of individual impact and its complicated moral, social and environmental justice implications. Instead, it has focused on highlighting how the dynamics of human demography have changed in the last 10 years, and how those changes have affected the biologically richest parts of the planet.

A logical reaction from the reader at this point may be to proclaim the situation hopeless and wonder if anything can really be done about the population issue. The short response is two-fold: (1) a certain amount of progress is already being made; and (2) there are several fairly non-controversial actions that can and should be taken to ensure that these positive changes continue and even accelerate. First, there are declines in fertility rates and shifts to more stable population structures (see Box 4.1) that are taking place in countries around the developing world. Part of these changes is the result of focused efforts on behalf of governments, international organizations and non-governmental organizations to extend health services, education, and access to family planning services to rural communities. Another part comes through urbanization and the improved access to infrastructure and government services that result when people either move to cities or when smaller settlements grow and become urbanized. Whatever the cause, people who live in urban areas tend to delay having children and reduce the number of children they have compared to their rural counterparts (UN 2008c). While there are numerous downsides to rapid urbanization, including localized environmental degradation, increased pollution, greater per capita resource use and urban poverty, the upside is a general improvement in economic and environmental indicators.

Second, with respect to actions that can be taken to ensure population growth rates continue to decline, three activities stand out: (1) address rural poverty in the developing world; (2) give girls and boys equal access to education; and (3) improve access to family planning and contraception. People who are desperately poor have a hard time taking care of themselves and their children, and the environment is far down the list of priorities. They frequently cannot make decisions in favor of safeguarding natural resources and the ecosystem services on which they depend if their health or basic nutritional needs are in doubt. Giving girls equal access to education has been shown repeatedly to promote equality, increase individual and family incomes and improve family and environmental health (Tembon and Fort 2008). Finally, improving access to family planning services, including contraception, has been shown to decrease poverty, reduce maternal and child mortality and improve environmental sustainability (Cleland et al. 2006). The delivery of such services, moreover, is not about promoting a social agenda, imposing fertility limits or providing controversial abortion services, rather it is about meeting the unmet contraceptive needs of men and women in keeping with the Millennium Development Goals established by the United Nations Development Programme (http://www.undp.org/mdg/basics.shtml) (UNFPA 2005).

Another action that we can take is to continue to establish and support protected areas for biodiversity and critical habitat. While some research indicates that protected areas act as poles of attraction for migration and population growth (Wittemyer et al. 2008), others dispute that claim (Joppa et al. 2009). Either way, the preponderance of evidence suggests that protected areas aid in safeguarding threatened species (Bruner et al. 2001; Brooks et al. 2009b). Even when parks do not function as planned, they have been found to act as deterrents to overharvesting and exploitation of natural resources (Rodriguez and Rodriguez-Clark 2001). A convincing argument has also been made in favor of getting urban centers to formally recognize and pay for the ecosystem services that protected areas and ecologically healthy rural areas provide to their inhabitants (Gutman 2007).

The concern with respect to the above actions is that population growth, while slowed, is still continuing. Also continuing are the habitat fragmentation and degradation associated with this growth. Given that the hotspots are composed of habitats and ecosystems that have already been reduced to a small fraction of their original extent, we cannot expect that the natural demographic transition will occur fast enough on its own to save these islands of biodiversity. We must assist that process by promoting strategies like the Millennium Development Goals, strengthening and building the global network of protected areas, and generally working on both parts of the equation: impact equals number of people multiplied by impact per person.

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Chapter 5
Vascular Plant Diversity in a Changing World: Global Centres and Biome-Specific Patterns

Jens Mutke, Jan Henning Sommer, Holger Kreft, Gerold Kier, and Wilhelm Barthlott

Abstract We summarize research on the global centres and gradients of vascular plant diversity. Most centres of plant species richness are located in geodiverse areas of the humid tropics and sub-tropics, especially in forest biomes. When focussing on the rarity of the flora, islands play an outstanding role. Endemism-scaled richness of oceanic island floras (endemism richness) exceeds those of mainland regions by several-fold. In contrast to the situation for most other groups of organisms, biodiversity patterns are relatively well understood for plants and vertebrates. However, plant diversity of some of the most important centres is still insufficiently documented – an important impediment for its conservation and sustainable use. Though habitat conversion and overexploitation have yet the most severe impact on plant diversity, future climate change is adding an additional threat. This will likely affect plant diversity, especially in low-latitude countries, which contributed least to the human-induced greenhouse gas emissions.

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5.1 Introduction

For the conservation, management, and use of biodiversity, it is essential to understand its spatial distribution on Earth. Plants are of special relevance in this context as primary producers and dominating elements in terrestrial ecosystems – there is no forest without trees, and no savannah without grass. On the other hand, plants together with terrestrial vertebrates are among the best-documented groups of organisms regarding their taxonomy, ecology, and distribution. Thus, the Global Strategy for Plant Conservation under the UN Convention on Biological Diversity suggested as one of its 16 targets, to protect 50% of the most important areas for plant diversity (IPA) by 2010. As documented in Table 5.1, for the global centres of plant species richness, this aim belongs to the long list of biodiversity conservation targets that have not been met.

The aim of this review is to present the global centres of vascular plant species richness, their abiotic environment, the human impact within these centres, as well as the biome-specific patterns of vascular plant species richness. In addition, we discuss possible biome-specific impacts of future climate change on plant diversity. The special role of islands as centres of high endemism richness is mentioned.

During the last decade, first assessments of global diversity patterns of most groups of land plants as well as, e.g. marine macroalgae have been published (Shaw et al. 2003; Adey 2005; Mutke and Barthlott 2005; Kerswell 2006; Feuerer and Hawksworth 2007; Hedenäs 2007; Konrat et al. 2008; Kreft et al. 2010). However, for many taxonomic groups, documented regional species numbers reflect mainly research intensity instead of real diversity patterns (e.g. Mutke and Geffert 2010). Until today, vascular plants, including ferns, gymnosperms, and flowering plants are still the only group with sufficient data to support more detailed analyses at least at the global scale. Thus, all analyses presented in this paper refer exclusively to this group.

Biodiversity patterns are highly scale dependent (Whittaker et al. 2001; Rahbek 2005). In several cases, the scale and spatial resolution of the study determines which of two geographical units harbours, e.g. higher species numbers (e.g. Braun et al. 2002; Schmiedel et al. 2010). Due to the global extent of the patterns reviewed in this chapter, we had to focus on vascular plant diversity at the landscape level – species richness per 10,000 km^2, and endemism richness of larger biogeographical units. Other datasets with information for hundreds of small scale vegetation plots have been established in recent years (Phillips and Miller 2002; Dengler and GIVD Steering Committee 2010). These can be used as the basis for further analyses referring to other spatial grain sizes including, e.g., patterns of beta-diversity (Condit et al. 2002).

5.2 Maxima, Centres, and Hotspots of Plant Diversity

There are several concepts and approaches to determine important areas for biodiversity conservation. Taking into account the fact that biological diversity has many different facets that might be measured, the simplest way is to look for maxima or

Table 5.1 Summary information about the 20 global centres of vascular plant species richness which surpass 3,000 species per 10,000 km^2

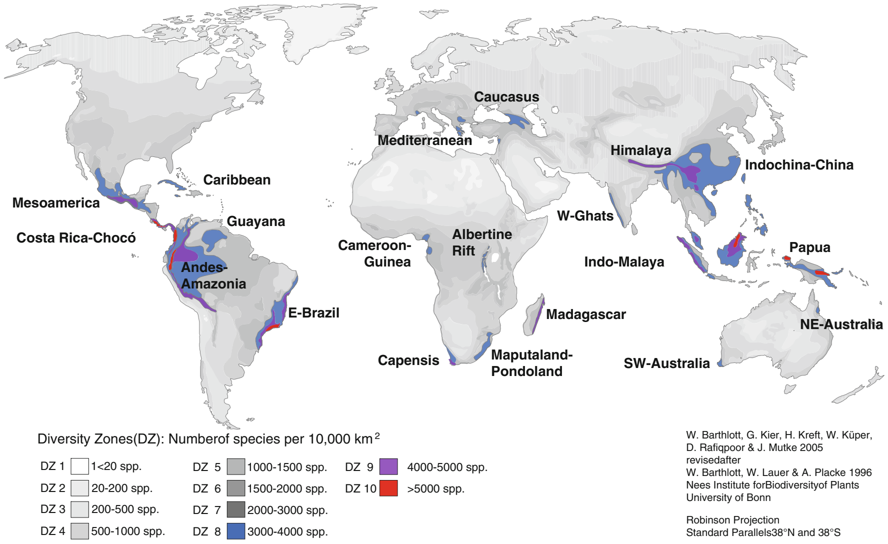
	Area size (1,000 km^2)	Human population density per km^2 [1]	% Area protected [2]	Biome [3] (see Figs. 5.2 and 5.3)	Elevat. range [m] [4]	Annual precip. [5] (Mean/Range) [mm]	Mean water balance [5] [mm]	Annual NPP [6] [g C/m]	Frost days [5]
Mesoamerica Centre	737.5	102.8	4.6%	3,2,1	5,600	1,351/4,462	14	763	0.0
Caribbean Centre	103.5	132.3	11.5%	2,1	2,250	1,384/1,736	48	823	0.0
Costa Rica-Chocó Centre	224.0	42.5	13.4%	1	3,500	3,603/6,646	1,559	972	0.0
Andes–Amazonia Centre	2,811.5	21.2	10.2%	1	6,300	2,376/5,883	872	1,020	0.0
Guayana Centre	379.0	0.7	61.7%	1,7	3,000	2,789/2,447	1,157	1,104	0.0
Eastern Brazil Centre	754.5	116.7	0.7%	1,7	2,800	1,333/2,849	190	923	0.0
Cameroon–Guinea Centre	88.5	74.4	11.1%	1	4,100	2,572/1,266	1,147	1,004	0.0
Albertine Rift Centre	55.5	177.1	10.5%	1,7	4,900	1,442/1,066	−18	1,138	0.0
Maputaland–Pondoland Centre	150.0	91.2	8.1%	10,7,1	2,250	816/702	−258	706	0.0
Capensis Centre	86.5	61.1	4.2%	12,13	2,250	327/1,030	−578	393	4.6
Madagascar Centre	91.0	48.0	5.3%	1	1,950	2,324/1,615	954	1,172	0.0
Mediterranean Centre	97.0	91.6	3.5%	12,4	3,200	746/997	−31	552	2.7
Caucasus Centre	170.0	65.9	9.1%	4,8	5,600	859/1,871	230	484	26.0
Himalaya Centre	125.0	65.6	24.7%	4,5,10	8,500	1,490/3,432	553	558	6.5
Western Ghats Centre	74.5	355.5	7.0%	1,2	2,600	2,758/4,280	896	779	0.0

(continued)

Table 5.1 (continued)

	Area size (1,000 km^2)	Human population density per km^2 [1]	% Area protected [2]	Biome [3] (see Figs. 5.2 and 5.3)	Elevat. range [m] [4]	Annual precip. [5] (Mean/Range) [mm]	Mean water balance [5] [mm]	Annual NPP [6] [g C/m]	Frost days [5]
Indochina–China Centre	2,528.5	196.9	3.4%	1,4	7,000	1,494/9,119	485	788	0.0
Indo-Malaya Centre	1,343.0	112.9	7.5%	1	4,100	2,750/3,079	1,302	1,129	0.0
Papua Centre	416.5	11.2	6.2%	1	5,050	3,289/6,033	1,316	1,120	0.0
Northeastern Australia Centre	11.0	8.4		7,1	1,600	1,604/2,687	289	850	1.6
Southwestern Australia Centre	27.5	2.1		1	650	901/544	−40	686	0.0
All Centres	10,275 (6.9% of land area)	total population: 939.6 Million	8.8%	91.7% area in forest biomes		703/9,700	−99.8	412.1	

This summary is based on data taken from [1] CIESIN and CIAT (2005), [2] UNEP and IUCN (2006), [3] Olson et al. (2001), [4] USGS (1996), [5] New et al. (2002), [6] Cramer et al. (1999)



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University of Bonn

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Standard Parallels38°N and 38°S

Fig. 5.1 Global map of species richness of vascular plants highlighting the 20 centres of highest species richness (after Barthlott et al. 2005; Mutke and Barthlott 2005)

centres of just one of these aspects, e.g. centres of species richness. This approach is used in most broad-scale biodiversity assessments including the map presented in Fig. 5.1. The main reason is that species richness is yet the only measure for which sufficient data are available with global coverage at the examined scale and resolution. On the other hand, many centres of species richness as presented in Fig. 5.1 are also important centres of plant diversity, in general. Centres of species richness, such as the Northern Andes, the South African Cape Region, or the Albertine Rift not only show a high concentration of species per area, but also have a high percentage of endemic taxa, are cradles for the rapid evolution of new species, and museums for the survival of evolutionarily old taxa (Fjeldså and Lovett 1997; Cowling and Proches 2005; Kier et al. 2009). Many of these areas are also important centres of origin of a number of economically important species (Vavilov 1926).

Centres of plant diversity that are also highly impacted by human influence, are denoted biodiversity hotspots, referring to a concept that was introduced by Norman Myers more than 20 years ago, and has gained much attention in global nature conservation policies (Myers 1988, 1990; Myers et al. 2000; Mittermeier et al. 2005). Most centres of vascular plant species richness depicted in Fig. 5.1 are as well global biodiversity hotspots (Kueper et al. 2004; Mutke and Barthlott 2005).

At the global scale, there exist 20 centres with at least 3,000 species per 10,000 km^2, which are described and analysed in detail by Barthlott et al. (2005). The top five centres with more than 5,000 species per 10,000 km^2 cover only 0.2% of the terrestrial surface, but are home to at least 18,500 endemic species (6.2% of the global flora): (1) the Costa Rica-Chocó Centre, (2) the Eastern Brazil Centre, (3) the Tropical Eastern Andes Centre, (4) the Northern Borneo Centre, and (5) the New

Guinea Centre. All these are located in the Neotropics or SE Asia. By contrast, species richness is lower in the African centres when compared with other parts of the tropics. This is also the case for the overall flora of the African continent. An exception is the Capensis Centre of South Africa, which almost reaches the global maximum species richness. Additionally, it has a highly unique flora with a high proportion of endemic species and even five endemic families (Goldblatt and Manning 2002).

5.3 Centres of High Vascular Plant Diversity Are As Well Centres of High Geodiversity

Most centres of vascular plant diversity are characterized by a high geodiversity, the diversity of the abiotic environment. This includes the diversity of the relief, soils, geology, or climate (Barthlott et al. 1996). Most of the centres are located in areas with high mountains, and often steep climatic gradients (Barthlott et al. 2005). All centres, except for the Australian ones, cover altitudinal ranges of at least 2,000 m, resulting in gradients from lowland to montane vegetation (Table 5.1). Together with the associated spatial heterogeneity of temperature and precipitation in these areas, these factors increase the floristic heterogeneity and consequently species richness on the examined spatial scale. The range between the driest and the wettest spot within each individual centre is at least 1,000 mm year^{-1} except for the SW Australia and Maputaland–Pondoland Centres. Referring to the generalized biome classification by WWF (Olson et al. 2001), more than 90% of the spatial extent of the centres fall into forest biomes. Sixteen of 20 centres belong to the tropical and subtropical moist broadleaf forest biome. Fifteen of 20 centres are located in humid areas, i.e. have positive water balances. Fifteen of 20 centres include areas, where there is no limitation of the thermal vegetation period, with exception of the NE Australia Centre, two centres with Mediterranean type climates, and the temperate Asian centres. However, most centres cover altitudinal gradients that reach the upper forest line and altitudes of frequent frost events. The high diversity of different soil types is regarded to be a special characteristic of the South African Capensis Centre (Goldblatt and Manning 2002). In addition to the current environmental parameters, historical influences play a major role. Many of the centres are either places of long-term climatic stability such as the South African Cape Region (Cowling and Proches 2005) or of important radiations within major groups of their flora due to recent tectonic events such as the Northern Andes (Gentry 1982).

5.4 Centres of Species Richness and Endemism: The Special Role of Mountains and Islands

Due to the high spatial heterogeneity of the abiotic environment, mountain regions provide a mosaic of many different habitats that facilitate the existence of different biological communities – often fairly isolated from other similar habitats. This island-like character of many mountain tops or isolated valleys has comparable effects on their floras as on oceanic islands. In an analysis of global patterns of 'endemism richness' of vascular plants and vertebrates, we found that all regions in the highest classes are either oceanic islands or mountain regions, especially in the tropics and sub-tropics (Kier et al. 2009). Endemism richness is calculated by summing up the fractions of the distribution ranges for all species covered by a mapping unit, and thus, reflects both endemism and species richness. The by far highest endemism richness of vascular plants per 10,000 km^2 occurs on the island of New Caledonia, followed by the South African Cape Region, Polynesia–Micronesia, the Eastern Pacific Islands, and the Atlantic Islands. Different parts of the tropical Andes of South America are as well within the top 20 regions of endemism richness of vascular plants (Kier et al. 2009). Around 70,000 vascular plant species, or c. 22% of the global flora, are endemic to oceanic islands on only 3.6% of the worldwide terrestrial surface (Kreft et al. 2008; Kier et al. 2009).

5.5 Human Impact Within Centres of Plant Diversity

Unfortunately, human impact on the world's ecosystems spatially coincides in many cases with patterns of biological diversity. Even conservative estimates based on the Global Landcover dataset generated by the European Joint Research Centre (2002) indicate that more than 40% of the land area has been converted by human land use in six of the 20 centres of vascular plant diversity (Caribbean Centre, Caucasus Centre, Eastern Brazil Centre, Mesoamerica Centre, Madagascar Centre, and Mediterranean Centre). Based on other habitat classifications and analyses, these figures are much higher (up to 80% and more) for all the 20 centres (Myers et al. 2000). Human population density and human impact as measured by the human footprint index (Sanderson et al. 2002) is on average higher within the 20 centres of vascular plant diversity compared with the global average. Based on 2005 population data (CIESIN and CIAT 2005), at least 939.6 million people live within the 20 centres of plant species richness listed in Table 5.1, resulting in an average population density that is more than twice the global mean. This might be partly due to the above-average net primary productivity (NPP) in these centres, which has been shown to correlate positively both with human settlement and with biological diversity at the examined scale (e.g. Balmford et al. 2001; Luck 2007). NPP is higher than the global average in all centres, except the Capensis. Conjointly with high geodiversity in most of the centres, these parameters not only correlate with high plant diversity, but also high cultural diversity (Stepp et al. 2005). Extremely high human population densities can be found, especially, in the Western Ghats Centre and parts of the Indochina–China Centre in Southern China, but as well in parts of the Albertine Rift Centre in Eastern Africa and of the Eastern Brazil Centre. On the other hand, diversity centres with only very sparse human settlement (good news areas) are, e.g. the Guayana Centre, parts of the lowland area of the Andes–Amazonia Centre, the SW and NE Australia Centres, the Karoo–Namib part of the South African Capensis Centre, and the Central Mountain Range of the Papua Centre.

Looking at the mean human population density (CIESIN and CIAT 2005) across the WWF biomes (Olson et al. 2001), highest densities occur in tropical coastal areas of the mangrove biome, the temperate broadleaf and mixed forest biome, the tropical and subtropical dry broadleaf forests biome, and the tropical and subtropical moist broadleaf forests biome. When analysed within biomes at ecoregion scale, a significant correlation between vascular plant species richness and human population density can only be found in five biomes: the boreal forests and taiga, the temperate grasslands, savannahs and shrublands, the montane grasslands and shrublands, the tundra and the deserts and xeric shrublands (Kier et al. 2005). These are the biomes, where plant growth is limited by constraints such as a short vegetation period or low water availability. Hence, in these biomes, human settlements concentrate in areas with suitable conditions for plant growth, and thus, for cultivation of crops, which often correlate with areas of high species richness (Kier et al. 2005).

5.6 Biome-Specific Patterns of Vascular Plant Diversity

In addition to centres of high diversity, there exist distinct plant diversity gradients linked to the abiotic environment. The best-known examples are latitudinal gradients of increasing species richness with decreasing latitude, or the importance of mountain areas (Fischer 1960; Pianka 1966; Gaston 2000; Willig et al. 2003; Hillebrand 2004; Sarr et al. 2005; Mutke 2011). The biome with the highest documented species richness is the tropical and subtropical moist broadleaf forest, followed by the tropical and subtropical coniferous forest, and Mediterranean woodlands and scrubs. Lowest mean species richness can be found in the tundra and taiga. However, the absolute minima of vascular plant species richness are located in arctic and Antarctic environments, as well as in hyper arid areas, e.g. of the Sahara. As shown in Fig. 5.2, the mean species richness per biome at a 10,000 km scale shows some relation to the length of the thermal vegetation period as well as to the number of humid months. In earlier, more detailed analyses, we always found those correlations with constraints imposed by the physical environment, such as the length of the thermal vegetation period or water availability (Mutke et al. 2001; Mutke and Barthlott 2005; Kreft and Jetz 2007; Kreft et al. 2008, 2010). However, it is still discussed to which extent current environment or earth history has been shaping these patterns (e.g. Ricklefs 2005).

5.7 Biome-Specific Impacts of Climate Change on Plant Diversity

There is no longer doubt that human activities are amplifying the rate of current global warming (Rahmstorf et al. 2007). According to the Intergovernmental Panel on Climate Change, estimates of the possible future economical and societal

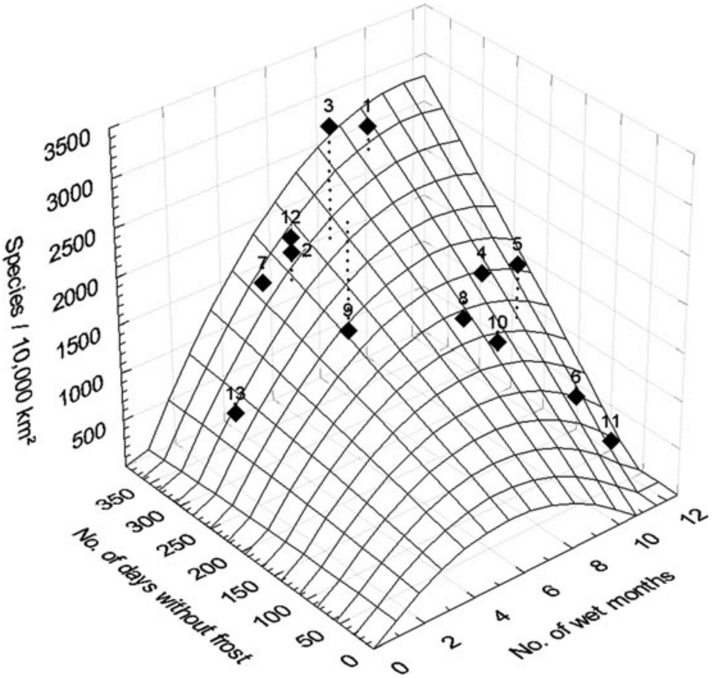

Fig. 5.2 Mean vascular plant species richness per 10,000 km^2 of the 14 terrestrial biomes in relation to frost-free days and number of wet months after Mutke (2011) based on the dataset used in Mutke and Barthlott (2005), biome definitions after Olson et al. (2001): (1) Tropical and subtropical moist broadleaf forests, (2) Tropical and subtropical dry broadleaf forests, (3) Tropical and subtropical coniferous forests, (4) Temperate broadleaf and mixed forests; (5) Temperate coniferous forests, (6) Boreal forests/taiga, (7) Tropical and subtropical grasslands, savannas, and shrublands, (8) Temperate grasslands, savannas, and shrublands, (9) Flooded grasslands and savannas, (10) Montane grasslands and shrublands, (11) Tundra, (12) Mediterranean forests, woodlands and scrub, (13) Deserts and xeric shrublands, and (14) Mangroves [not included in our analysis)]

development indicate a continuation of global warming at even accelerating rates at least until the year 2100 (IPCC 2007).

Habitat conversion, overexploitation, pollution, and invasive alien species have been important drivers of biodiversity loss in the past and will be in the future (Millenium Ecosystems Assesement 2005; Convention on Biological Diversity 2010). However, life on earth is increasingly affected by changing climatic conditions in many different ways (Walther et al. 2002; Parmesan 2006; Convention on Biological Diversity 2010). Earlier flowering times and arrival of migratory birds have been observed that are in concordance with warmer spring temperatures in parts of the northern hemisphere. Climate change may also have an effect on the size and location of species' geographic ranges (Parmesan 2006). This includes the expansion of ranges into new, suitable areas that may be located at higher latitudes and/or altitudes. On the other hand, species may get locally extinct in areas where the climatic changes exceed their ecological and physiological adaptability (Parmesan 2006).

The limitation in data availability on individual plant species distributions on a global scale calls for alternative concepts to assess the impact of climate change at this level. One way to tackle this challenge is to analyse the contemporary relationship between regional species richness and the corresponding climate conditions. Thereby, the occurrence of a certain set of climate variables can be translated in a corresponding capacity for species richness (CSR) for that region. According to the space-for-time substitution concept (La Sorte et al. 2009), this relationship is then applied to estimated future climate surfaces (Sommer et al. 2010).

In a global model for contemporary plant species richness, the relationship between temperature and water availability appeared to be a major limiting factor of the species number a certain region can maintain (Kreft and Jetz 2007; Sommer et al. 2010). In areas with humid conditions, a positive relationship between species richness and temperature was found, i.e. the warmer the temperature, the higher the corresponding species richness. In dry regions, the correlation between species richness and temperature appeared to be negative; here, hotter regions maintain fewer species than cooler ones.

In the context of climate change, this relationship may provoke substantial shifts in the regional capacities for species richness (CSR, compare Fig. 5.3 with Sommer et al. 2010) and the CSR may increase in areas that feature cool and wet climates. On the other hand, CSR may substantially decrease in already warmer and dryer

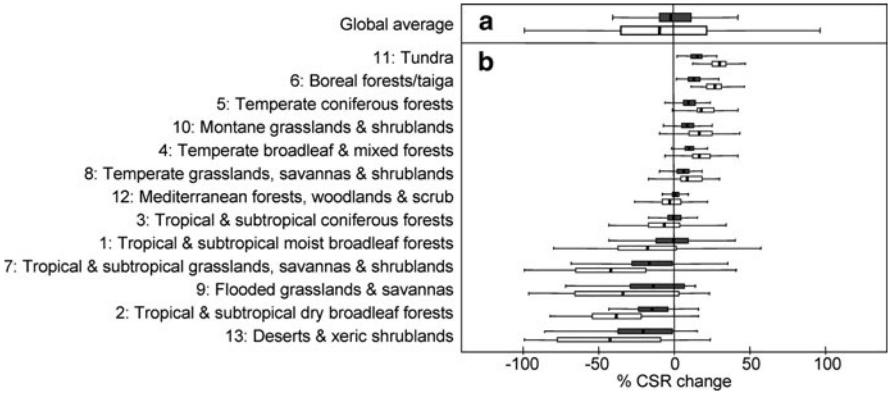

Fig. 5.3 Modelled changes in the capacity for species richness (CSR) between today and the year 2100 under the IPCC scenarios B1 (grey: +1.8°C) and A1FI (white: +4.0°C) (modified after Sommer et al. 2010). (**a**) Global average CSR change as mean values for the PCM, CGCM2, CSIRO2, and HadCM3 general circulation models (GCMs). (**b**) CSR change across all 13 terrestrial biomes. Percentage values reflect the change in CSR for the respective subset of 110 × 110 km equal-area grid cells. *Bold lines* indicate the mean value, *boxes* indicate second and third quartiles, and whiskers indicate 10th and 90th percentiles

subtropical and tropical regions. This is particularly alarming, as developing countries that contributed less to the global greenhouse gas emissions are subject to the most severe changes in the CSR, but are in many cases particularly vulnerable to the consequences of climate change (Intergovernmental Panel on Climate Change 2007).

5.8 Hotspots of Plant Diversity: Well Known But Poorly Documented

As documented by a large number of publications during the last 15 years, the location of the main centres of diversity of vascular plants and vertebrates are well known on the global scale (Kier et al. 2005; Mutke and Barthlott 2005; Ceballos and Ehrlich 2006; Grenyer et al. 2006; Barthlott et al. 2007; Jetz et al. 2009; Kier et al. 2009). There is a far reaching consensus among scientists on a global minimum set of irreplaceable key biodiversity areas, where conservation would be most effective (Brooks et al. 2006). There is no excuse for the fact that environmental degradation continues and is even accelerating at many of these sites.

However, despite the fact that it is well-known that, e.g. the floras of Colombia in NW South America or New Guinea in SE Asia are remarkably diverse, the state of floristic knowledge is often biased either taxonomically or geographically. Frodin (2001) lists these regions among his global compilation of “areas that most need floras”. In the 1990s, it was estimated that around 25% of the Neotropical flora consists of yet undescribed species (Dirzo and Gómez 1996; Thomas 1999). Kueper et al. (2006) found that some of the top centres of vascular plant diversity in tropical Africa are among the least documented regions. Regarding global diversity patterns of mosses, we recently showed that many floras outside Europe are heavily undersampled (Mutke and Geffert 2010). Thus, the conservation of biodiversity and our biological resources on a sound scientific basis requires further basic taxonomic research, natural history collections, and the respective field work. However, especially for hotspot areas with high plant diversity combined with high impact by human activities, the loss of biological diversity most likely exceeds by far the rate of its documentation. As our traditional efforts in this context might be insufficient, new innovative methods may be helpful including DNA barcoding (Hollingsworth et al. 2009), GIS-based geostatistical modelling and gap analyses (Burgess et al. 2002; Burgess et al. 2005; Paton 2009). Moreover, it is important that non-commercial biodiversity research and international co-operation to document the vanishing biodiversity and to understand ecosystem functions is not impeded by political restrictions. It is essential to build and maintain true co-operations that result in important benefits for all partners – though these might only be partly monetary. Data sharing, capacity building regarding training and education, and the establishment of research infrastructure are strongly needed.

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Chapter 6
Genetic Basis of Human Biodiversity: An Update

Guido Barbujani and Vincenza Colonna

Abstract The massive efforts to study the human genome in detail have produced extraordinary amounts of genetic data. Although we still fail to understand the molecular bases of most complex traits, including many common diseases, we now have a clearer idea of the degree of genetic resemblance between humans and other primate species. We also know that humans are genetically very close to each other, indeed more than any other primates, that most of our genetic diversity is accounted for by individual differences within populations, and that only a small fraction of the species' genetic variance falls between populations and geographic groups thereof. However, population differences are large enough for patterns to emerge, and these patterns have been extremely useful to reconstruct the history of human migration and to recognise the effects of reproductive isolation. In many cases, crucial information about human demographic history has emerged from multidisciplinary analyses, which have stressed the importance of cultural, as well as geographical, barriers in causing local divergence of populations.

6.1 Introduction

Our knowledge of human genome diversity has greatly improved in the last decades, partly as a side effect of the effort to understand the basis of human disease. The Human Genome Project, begun in 1990 and coordinated by the US

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Department of Energy and the National Institutes of Health (Watson and Jordan 1989), had several ambitious goals, mostly related with molecular medicine. They included identification of all genes in human DNA and determination of the nucleotide sequence of the 46 chromosomes. The human reference sequence, or NCBI sequence, which in fact is an assemblage of haploid DNA segments from five donors (International Human Genome Sequencing Consortium 2001) is publicly available at Genbank (Benson et al. 2010).

Now that the whole genome sequences of nine individuals are available, and studies of >1 million polymorphisms have been published by the hundreds (Ragoussis 2009), we have a much better understanding of why single-gene diseases arise, and how alleles at modifier genes affect the severity of the symptoms. In addition, nucleotide substitutions have been identified accounting for a large share of the observed variation for simple non-pathological traits, such as lactose tolerance (Tishkoff et al. 2007; Enattah et al. 2008) and taste perception (Garcia-Bailo et al. 2009). However, we still miss a comprehensive picture of the molecular basis of many phenotypic traits. These include quantitative traits such as adult height (Weedon et al. 2008), or the difficult-to-define, but important, “healthy aging” (Glatt et al. 2007), and most common disorders, from cancer to cardiovascular and neurological diseases (Goldstein 2009). The problem is that these phenotypes result from the action of tens or hundreds of genes, most of them with small effects, often influenced by scores of environmental factors. Dealing with such levels of complexity requires not only abundant data, which are rapidly being produced, but also good models predicting how hundreds of genetic and non-genetic factors interact, which we have not developed yet.

In the meantime, however, the recently published data are giving us an unprecedented depth of insight into human diversity, which in turn allows for more robust inferences about the underlying demographic history. The present paper will deal with some of these recent advancements.

6.2 Patterns of Human Genetic Diversity

6.2.1 *Genetic Diversity Between Humans and Our Closest Relatives*

At the protein level, humans are closely related with chimpanzees, and a little bit less closely with gorillas (Goldman et al. 1987). The chromosomes, and the general arrangement of genes on them, are strikingly similar in humans and in the great African apes (Jauch et al. 1992), to the point that according to Gagneux and Varki (2001) all these species could conceivably be classified as a single genus. At the DNA level, results depend on the type of polymorphism considered. Broadly speaking, variable sites are classified either as single nucleotide polymorphisms (SNPs) or structural variants, the latter including a vast and heterogeneous set of microsatellite polymorphisms, insertion/deletions, block substitutions, inversions and copy number variations (CNVs) (Frazer et al. 2009). Various chromosomal rearrangements, millions of insertion/deletion (indel) events, and roughly 35 million single-nucleotide changes were identified by aligning complete (or almost complete) human and chimpanzee genomes (Chimpanzee Sequencing and Analysis Consortium 2005). Over an estimated genome length close to three billion nucleotides, the last figure means that the rate of single-nucleotide substitutions is 1.23%, 1.06% of which apparently fixed between species.

However, that figure might underestimate the actual level of species differentiation. Indeed, the DNA regions containing segmental duplications, or SDs, are difficult to align between humans and chimpanzees (Marques-Bonet et al. 2009b). Some 150 Mb of genomic DNA sequence is estimated to be present only in one or the other species (Kehrer-Sawatzki and Cooper 2007). Thus, the between-species difference in duplication content and copy number is close to 2.5% of the total genome length (Cheng et al. 2005), twice as much as inferred from single-nucleotide substitutions. These figures are approximate and may change in the future, but highlight how the apparent divergence may differ, sometimes deeply, depending on the polymorphism considered and on the mutation mechanism generating it (Marques-Bonet et al. 2009a).

6.2.2 Low Levels of Genetic Diversity Within Humans

The comparison between humans and other primates offers another important insight into the genetic peculiarities of our species. The branches of the evolutionary tree separating humans are very short, shorter indeed than those between chimpanzees of the same geographical region (Fig. 6.1). In various genome regions,

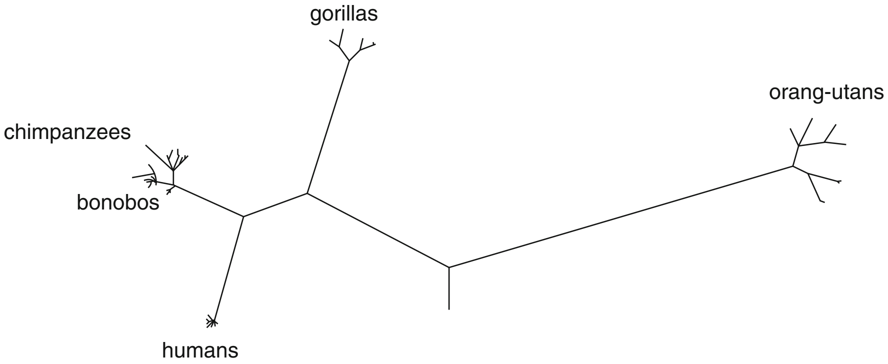

Fig. 6.1 Phylogenetic tree of human ($n = 70$), chimpanzee ($n = 30$), bonobo ($n = 5$), gorilla ($n = 11$) and orang-utan ($n = 14$), based on 10,000 bp sequences of a noncoding Xq13.3 region. A gibbon sequence was used as outgroup. Reproduced with permission, from Kaessmann et al. (2001)

nuclear (Kaessmann et al. 2001) as well as mitochondrial (Gagneux and Varki 2001), humans appear far less differentiated than any other related species, including bonobos. This conclusion is supported by several lines of evidence.

In fact, if we subtract 1.06% (the nucleotide substitutions fixed between species) from 1.23% (the estimated SNP difference between humans and chimpanzees), the maximum extent of SNP in the human genome is 0.17%. This figure can be compared with measures of SNP variation among the nine complete genome sequences available so far (Levy et al. 2007; Bentley et al. 2008; Wang et al. 2008; Wheeler et al. 2008; Ahn et al. 2009; Kim et al. 2009; McKernan et al. 2009; Schuster et al. 2010), plus the NCBI reference sequence.

In the study of Craig Venter's genome, 3,213,401 of the 4.1 million variants detected (including structural variants) were defined as single-nucleotide variable sites (Levy et al. 2007). More than 1.5 million additional SNPs were described in the most recent study on Southern Africans, based on two completely sequenced genomes, and three genomes massively sequenced in coding regions (Schuster et al. 2010). Therefore, allowing for some inaccuracies to exist in the data, over an estimated genome length close to three billion, SNPs appear to represent some 0.13% of the total. As further studies will expand the list of polymorphic sites, estimates based on whole genome comparisons may approach the estimates inferred from species comparisons. Even then, the genetic differences between two random humans would be roughly half of those between two random chimpanzees (Fischer et al. 2004).

6.2.3 Summary Measures of Population Structure

The pattern of genetic differences over the geographical space is referred to as population structure, and can be summarised in several ways. The simplest is by means of Wright's F_{ST}, representing in this case the fraction of the overall species' variance explained by differences between populations.

Different loci vary in their F_{ST} values. Regions of high and low differentiation are scattered over the chromosomes (Weir et al. 2005; Coop et al. 2009), and the standard deviation of F_{ST} equals or exceeds the average estimate, thus suggesting that averages do not well represent the whole pattern. Nevertheless, these averages appear rather consistent, somewhere between 0.05 and 0.13 (International Hap Map Consortium 2005; Barreiro et al. 2008; Li et al. 2008; Auton et al. 2009; Xing et al. 2009) for autosomal SNPs (Table 6.1), i.e. one-third of what observed in gorillas, 0.38 (Thalmann et al. 2007). A comparison with chimpanzees is only possible for Y-chromosome SNPs, but once again F_{ST} in humans is about one-third (0.36 versus 0.88), even though humans, unlike chimpanzees and gorillas, are spread all over the world (Stone et al. 2002). Therefore, not only do humans show the lowest species diversity among primates (Kaessmann et al. 2001), but they are also subdivided in populations more closely related than any other primate species, with the possible exception of bonobos (Fischer et al. 2006).

Table 6.1 Genomic estimates of F_{ST} for the global human population[a]

N of markers	Samples	F_{ST}	Reference
599,356 SNPs	209 individuals from four populations: Caucasian, Chinese, Japanese, Yoruba	0.13	Weir et al. (2005)
1,034,741 SNPs	71 individuals from four populations: Caucasian, Chinese, Japanese, Yoruba	0.10	Weir et al. (2005)
1,007,329 SNPs	269 individuals from four populations: Caucasian, Chinese, Japanese, Yoruba	0.12	International Hap Map Consortium (2005)
443,434 SNPs	3,845 worldwide distributed individuals	0.052	Auton et al. (2009)
2,841,354 SNPs	210 individuals from 4 populations: Caucasian, Chinese, Japanese, Yoruba	0.11	Barreiro et al. (2008)
243,855 SNPs	554 individuals from 27 worldwide populations	0.123	Xing et al. (2009)
100 Alu insertions	710 individuals from 23 worldwide populations	0.095	Watkins et al. (2008)
67 CNVs	270 individuals from four populations with ancestry in Europe, Africa or Asia	0.11	Redon et al. (2006)

[a] *SNP* single nucleotide polymorphism, *CNV* copy number variation

Many structural changes in the genome result in CNV , and occur at a much lower rate than single-nucleotide substitutions. Accordingly, one should not necessarily expect similar levels of diversity for SNPs and CNVs. However, the F_{ST} estimate for 67 autosomal CNVs (in a small set of populations) is 0.11 (Redon et al. 2006), i.e. just a bit less than most SNP-based estimates. Similar levels of population differentiation, around 0.09 or 0.10, were inferred from studies of Alu insertions (Redon et al. 2006; Xing et al. 2009).

A more articulate way to describe population structure is by means of statistics apportioning the genetic variance at various levels of population subdivision, using forms of analysis of variance, such as AMOVA (Excoffier et al. 1992) that take into account the fact that the allele-frequency distributions are not Normal (Table 6.2). Lewontin (1972) pioneered this type of work, analysing blood group and serum proteins in seven racial groups (Caucasian, African, Mongoloid, S. Asian Aborigines, Amerinds, Oceanians and Australian Aborigines). He estimated that differences among populations of the same group, and between groups, account, respectively, for 8.3% and 6.3% of the global species variance. Because the remaining 85.4% of the variance was accounted for by differences between individuals of the same group, Lewontin proposed to abandon the concept of biological race as useless for the study of humans. Understandably, this proposal met with criticism, and one was that there were problems in the interpretation of the statistics chosen to quantify diversity. However, when Lewontin's data (with one additional locus) were reanalysed using a different metrics, the initial results were confirmed (Latter 1980).

Later DNA studies, generally grouping populations under geographic, rather than racial, criteria, confirmed that human genome diversity may be summarised by three numbers, 85, 5 and 10, representing, respectively, the percent individual differences within populations, between populations of the same group and between groups (Barbujani et al. 1997; Jorde et al. 2000; Rosenberg et al. 2002; Bastos-

Table 6.2 Estimated fractions of the global human diversity, at three hierarchical levels of population subdivision (estimates based on only mtDNA or the Y chromosome not reported)[a]

Polymorphism	N of loci	Within populations	Between populations, within groups	Between groups	Reference
Protein	17	85.4	8.3	6.3	Lewontin (1972)
Protein	18	85.5	5.5	9.0	Latter (1980)
Protein	25	86.0	2.8	11.2	Ryman (1983)
SNPs	79	84.5	3.9	11.7	Barbujani et al. (1997)
STRs	30	84.5	5.5	10.0	Barbujani et al. (1997)
STRs	60	87.9	1.7	10.4	Jorde et al. (2000)
SNPs	30	85.5	1.3	13.2	Jorde et al. (2000)
Alu insertions	13	80.9	1.8	17.4	Jorde et al. (2000)
Alu insertions	21	82.9	8.2	8.9	Romualdi et al. (2002)
β-globin	1	79.4	2.8	17.8	Romualdi et al. (2002)
STRs	377	94.1	2.4	3.6	Rosenberg et al. (2002)
STRs	377	87.6	3.1	9.2	Excoffier and Hamilton (2003)
X-linked STRs	17	90.4	4.6	4.9	Ramachandran et al. (2004)
Indels	40	85.7	2.3	12.1	Bastos-Rodrigues et al. (2006)
HLA	5	88.6	4.4	7.0	Meyer et al. (2006)
Autosomal SNPs	642,690	88.9	2.1	9.0	Li et al. (2008)
X-linked SNPs	16,400	84.7	2.4	12.9	Li et al. (2008)
MEDIAN[b]		87.0	2.8	10.2	

[a] *SNP* single nucleotide polymorphism, *STR* short tandem repeat, *Indel* insertion/deletion polymorphism

[b] These are the median values calculated giving the same weight to all studies. Otherwise, given the large differences in the number of loci considered, the weighted medians would correspond to the values estimated by Li et al. (2008). The actual median values, respectively, 85.5, 2.8 and 10.0, did not sum up to 1, and hence they were normalised by dividing them by 98.3

Rodrigues et al. 2006; Li et al. 2008). Very similar estimates were inferred from autosomal studies of SNP and short tandem repeat (STR) variation, and some of them included loci such as beta-globin (Romualdi et al. 2002) and HLA (Meyer et al. 2006), known to be affected by selection. This result is intriguing, because natural selection affects single loci, and therefore it is expected to increase (diversifying selection) or reduce (stabilising selection) the value of F_{ST} at specific genomic regions (Cavalli-Sforza 1966); many modern approaches for the identification of differential selection are indeed based upon this principle (Novembre and Di Rienzo 2009). Apparently, the differences between neutral loci and selected loci are minor, and do not alter substantially the general pattern of geographic variation observed over much of the genome.

Analyses of mtDNA and Y-chromosome polymorphisms yield higher estimates of between-population and between-group variance (reviewed in Brown and Armelagos 2001 and Barbujani 2005), strongly suggesting that genetic variances largely reflect the interplay between drift and gene flow, with drift obviously having a greater impact upon the haploid portions of the genome. Conversely, a higher estimate of the degree of differentiation within populations, 88.9%, comes from the largest study so far, more than 640,000 autosomal SNPs (Li et al. 2008). In short, population differences account for 15% or less of the species' genetic variance, both when estimated by F_{ST} and by summing up the last two columns of Table 6.2. One way to envisage these figures is to say that the expected genetic difference between unrelated individuals from distant places exceeds by 15% the expected difference between members of the same community (Barbujani 2005). Another is to say that if only one human population survived extinction, about 85% of the species' allelic diversity would be retained (or more, if the surviving population is African).

6.3 How Did We Traditionally Envisage Human Diversity?

The results summarised above go contrary to the traditional, and still widespread, idea that humans can be easily attributed to natural biological clusters, members of which have closer genealogical relationships with each other than with members of other clusters. For centuries, these clusters have been referred to as races, but very old is also the suspicion that there might be something unscientific in human racial classification. Man, wrote Charles Darwin (1871), "has been studied more carefully than any other animal, and yet there is the greatest possible diversity amongst capable judges whether he should be classed as a single species or race, or as two (Virey), as three (Jacquinot), as four (Kant), five (Blumenbach), six (Buffon), seven (Hunter), eight (Agassiz), eleven (Pickering), fifteen (Bory St. Vincent), sixteen (Desmoulins), twenty-two (Morton), sixty (Crawfurd), or as sixty-three, according to Burke". When these words were written, systematic studies of human biological diversity were just analyses of skull shape and size, and genetics was in its infancy. Still, after the accumulation of enormous amounts of relevant information, the levels of uncertainty have not decreased by much. The obvious biological differences among humans allow one to make educated guesses about an unknown person's ancestry, but agreeing on a catalogue of human races has so far proved impossible.

Of course, we all are not equal. The classical, *typological* approach consists in identifying some basic human types, defined on the basis of facial traits, height, body structure and skin colour, and then assigning individuals to one of those types, or races (Cohen 1991). Starting with Linnaeus and for at least two centuries, analyses of human biological diversity were essentially aimed at compiling race catalogues (Bernasconi and Lott 2000). However, as Frank Livingstone (1963) pointed out, it is simple to list typical anatomical features of a region or a population, but each human group includes variable proportions of people who do not resemble the typical individual. To bypass this difficulty, races were defined by combinations of trait, often including non-biological variables such as language, house-building and tool-making techniques (see Cohen 1991, where reference to the original eighteenth and nineteenth century sources can be found). However, there is a second problem, namely, variation is discordant across traits, and so analyses of different sets of traits lead to different classifications. A third problem, of which we became aware only more recently, is that there is no general "common perception" of race; individuals who are regarded as white in a certain cultural contexts (e.g. in India) may be considered black in another (e.g. in Europe or North America) (Glasgow 2009). It comes as no surprise, then, that the scientific attempts to list the main human groups yielded many discordant catalogues, including from 2 to 200 items (Molnar 1998).

Starting from Linnaeus' six races and going through Buffon's, Blumenbach's, Cuvier's and many other systems into the twentieth century, the number of races increased (see Madrigal and Barbujani 2007 for a more detailed list). In his *Systema naturae*, Linnaeus first defined the species *Homo sapiens* within the order Primates and divided it in four continental varieties. At the end of the eighteenth century, it was the German anatomist Blumenbach who refused a relationship between humans and the other primates, proposing that there are five human races, corresponding to the five continents, four of them regarded as more or less serious degenerations from the European race, which he first termed "Caucasian".

In the nineteenth and early twentieth century, the picture became increasingly complicated. Fitting the populations newly encountered by explorers and anthropologists into pre-existing races proved difficult, and new races had to be added. The catalogues became broader, and the distinctions between races therein ambiguous, until Livingstone (1962) proposed that human variation should be regarded as essentially continuous, and the concept of race be regarded as misleading for understanding human biological diversity. Dobzhansky (1967) maintained that human races could nevertheless be defined at least as open genetic systems, each differing from its neighbours for some allele frequencies. However, according to this definition any human population would be a distinct race, which is not how races are generally conceived by evolutionary biologists. This debate is still open, with different authors siding with either Dobzhansky or Livingstone. However, in the Sixties genetic information had substantially grown, as well as quantitative methods for its analysis (Cavalli-Sforza and Edwards 1967; Cavalli-Sforza 1966; Sokal et al. 1988). Starting from the last decades of the twentieth century, most studies focussed, then, on the levels and patterns of genetic variation in geographical space, summarised in Cavalli-Sforza et al. (1994) atlas.

6.4 How Do We Summarise Human Diversity, and How Did It Evolve?

Recent studies of the human genome are showing why it proved so difficult to agree on a list of the main biological groups of humankind. To understand the main evolutionary processes shaping human diversity, one should focus on samples of populations that have been affected only mildly by the migratory exchanges of the last few centuries; these are what we shall call *anthropological* samples, and are represented by individuals from relatively isolated groups. Many such samples were collected at the CEPH (Centre d'Etude du Polymorphisme Humain, Paris), where they form the HGDP (Human Genome Diversity Panel) (Cann et al. 2002; Cavalli-Sforza 2005), namely, a set of cultured cell lines from >1,000 individuals in 51 worldwide populations, with the exceptions of India and Australia (http://www.cephb.fr/en/hgdp/diversity.php/).

To place in the appropriate context the results of genetic studies, it is also useful to remind that the fossil record shows clear evidence of an origin of anatomically modern humans in Africa, some 200,000 years ago (Lahr and Foley 1994). This human form dispersed from Africa, largely (Wolpoff et al. 2001; Relethford 2008) or completely (Foley 1998; Tattersall 2009) replacing all pre-existing human forms in Europe and Asia, respectively, Neandertals and *Homo erectus*, and possibly other human forms we do not know, or do not have a name, yet (Krause et al. 2010). The first paleontological or archaeological evidence of human presence in the Americas (perhaps 15,000 years ago: Greenberg et al. 1986; Goebel et al. 2008) and Oceania (starting perhaps 3,000 years ago: Terrell et al. 2001; Diamond and Bellwood 2003) is relatively recent, whereas island Melanesia was reached relatively early (40,000 years ago: O'Connell and Allen 2004).

6.4.1 Clinal Variation Is the Rule

Classical studies of allele frequencies in anthropological samples have shown that a large share of human genetic variation is distributed in gradients over the geographical space (Menozzi et al. 1978; Sokal et al. 1990). These gradients are obvious, broad and detectable for many loci in Europe and Asia (Barbujani and Pilastro 1993), less so in the Americas (O'Rourke and Suarez 1985; Rothhammer et al. 1997) and in Africa (Reed and Tishkoff 2006). At the DNA level, patterns inferred from the Y-chromosome and autosomal polymorphisms are generally clinal, and hence similar to those identified for allele frequencies (Chikhi et al. 1998; Semino et al. 2000) but those inferred from mtDNA are not (Simoni et al. 2000; Soares et al. 2010).

Not only allele frequencies, but indeed many indexes of genetic diversity form similar, worldwide clines. In two studies of the same set of 783 STR loci from the CEPH-HGD panel, geographic distances between populations were calculated along obligate waypoints, representing plausible migration routes within landmasses. In agreement with the hypothesis of repeated founder effects during dispersal from Africa into the rest of the world, measures of both genetic distance from the African populations (Ramachandran et al. 2005) and of internal genetic diversity (Liu et al. 2006) showed a strong correlation with geography. Ramachandran et al. (2005) then went forward, assuming >4,200 possible places of origin of the African expansion and testing how the correlation between genetic and geographic distances changes depending on the origin of the expansion. The best fit was obtained for an origin close to the gulf of Guinea, in an area where, however, data are missing. An origin in Eastern or Southern Africa, followed by repeated founder effects, is the most parsimonious hypothesis accounting for the distribution of skull shapes, for morphological diversity declines with distance from Africa, in parallel with genetic diversity (Manica et al. 2007). Studies of 650,000 markers, SNPs in this case, essentially confirmed these results (Biswas et al. 2009), and added to the picture an increase of linkage disequilibrium in populations at increasing distances from Africa (Li et al. 2008).

These extensive gradients have been compared with the pattern of neutral genetic variation predicted by either isolation by distance, or by models incorporating founder effects (Hunley et al. 2009). The simulated scenario best reproducing the observed diversity was one, in which populations went through a number of fissions, bottlenecks and long-range migrations as new territories were colonised, while exchanging migrants within limited distances.

In short, human genetic diversity seems shaped by phenomena occurring in geographic space, i.e. demographic expansions. Many studies have highlighted the effects of natural selection upon specific regions of the genome, and there is no doubt that a fraction of human genome diversity does indeed reflect adaptation (Sabeti et al. 2006; Harris and Meyer 2006). However, the patterns shown by genome regions known to be subjected to selective pressures suggest that such pressures are often weak, so much so that the geographic distribution of selected alleles seems to basically reflect episodes in population history rather than selection itself (Balaresque et al. 2007; Coop et al. 2009; Hofer et al. 2009). The genetic exchanges occurred in the course of the frequent contacts have resulted in a smooth, continuous variation of many genetic parameters. As a consequence, zones of sharp genetic change are not the rule, but the exception; most human populations are not surrounded by clear genetic boundaries. This is one reason why defining genetically discrete groups in humans has proved so challenging.

6.4.2 A Recent Exit from Africa

Instead of inferring the place of origin of the human expansion from the data, Liu et al. (2006) chose an arbitrary point in Ethiopia, and could thus estimate the likely date of the earliest human dispersal from Africa. In practise, that was the date maximising the overlap between observed and simulated genetic data, the latter generated assuming that small groups of founders moved centrifugally from one locality to the next and then grew in numbers, until the territory carrying capacity was reached and another migratory step became necessary. The best fit was observed for an expansion starting 56,000 years ago, from a founding population of $\sim$1,000 effective individuals who grew rapidly in numbers each time new territory (and the relative resources) became available. The main outliers, showing excess genetic divergence, were populations of South America, known to have evolved in extreme isolation, and therefore strongly subjected to drift (Rosenberg et al. 2002).

Estimates of the likely date of exit from Africa vary depending on the genetic markers and populations considered, but seem to indicate a more recent time than previously thought, between 65,000 (Macaulay et al. 2005) and 51,000 years ago (Fagundes et al. 2007). An independent confirmation of this timescale comes from the study of a human parasite, the bacterium *Helicobacter pylori*, where the decline of genetic diversity at increasing distances from Africa appears compatible with a dispersal process starting 58,000 years ago (Linz et al. 2007).

Comparisons of the available data with those generated by simulation under explicit demographic models clearly support a series of recent founder effects in an expanding population over all alternative models (Fagundes et al. 2007; Deshpande et al. 2009; Degiorgio et al. 2009). These studies also provide important insight into the possible interactions between anatomically modern and anatomically archaic populations. Indeed, the genetic effects of admixture with the genomes of anatomically archaic humans would have resulted in a very different pattern of variation, incompatible in fact with the observed one (Degiorgio et al. 2009). Accordingly, even though it is impossible to rule out any degree of introgression from anatomically archaic humans into the modern gene pool (Relethford 2008), we can at least conclude that introgression, if any, was minimal. This view is independently supported by the available ancient DNA evidence. Although, for technical reasons, ancient sample sizes are small, and the markers essentially limited to mitochondrial DNA, there is no evidence of a possible genealogical continuity between Neandertals and modern Europeans (Currat and Excoffier 2004), whereas sequences of anatomically modern Europeans who lived in temporal proximity to the Neandertals, the Cro-Magnoid, fit well in the modern Europeans' genealogy (Belle et al. 2009). The first analysis of the Neandertal nuclear genome seems to suggest that there was indeed some degree of gene flow from Neandertals into the ancestors of modern Eurasian (but not African) people (Green et al. 2010), but alternative explanations not involving admixture exist (see e.g. Ghirotto et al. 2011).

6.4.3 Africa Is Genetically Special

In a large study of genotypes, haplotypes and CNVs (525,910 SNPs and 396 CNV sites), Jakobsson et al. (2008) asked which proportion of those polymorphisms are shared in different continents. At the level of the individual SNPs, and correcting for the different sample sizes, 81.2% of the SNPs appeared to be cosmopolitan, i.e. present, at different frequencies, in all continents. Less than 1% were specific to a single continent, and 0.06% were observed only in Eurasia, which was kept separate from East Asia in these analyses. Things changed when alleles were combined in haplotypes, but not radically so. The fraction of cosmopolitan haplotypes decreased to 12.4%, whereas 18% of the haplotypes appeared to be exclusively African. However, once again continent-specific features were a minor fraction of the total, because exclusively Eurasian, East Asian, American and Oceanian haplotypes summed up to just 11% of the total. As for CNVs, there is a greater proportion of continent-specific polymorphisms, although the high frequency of Eurasian CNVs (5.7%) raises the doubt that there might be some bias in the selection of the polymorphisms.

Sequencing of long stretches of DNA in smaller samples had already suggested that a large fraction of human haplotype blocks are either specifically African or generically human (Gabriel et al. 2002), with very few features pointing to an Asian or European origin. A clear example of the implications of this extensive sharing of polymorphisms across the world comes from comparisons of completely sequenced genomes. Craig Venter's (Levy et al. 2007) and James Watson's (Wheeler et al. 2008) genomes share fewer SNPs, 461,000, than either of them shares with Seong-Jin Kim's (Ahn et al. 2009), respectively, 569,000 and 481,000. Clearly, these numbers do not represent what we would observe, on average, in a broad comparison of Korean and European people. However, they show that the large genetic variation within populations causes some individuals of similar origin, Watson and Venter in this case, to resemble each other less than each resembles some individuals from another continent. Similarly, comparisons of complete sequences of the DNA coding regions (exome) show that differences within Africa, and even within a single population, the San, are often greater than those between people from different continents; on average, two San differ for 1.2 nucleotides per kilobase, versus 1.0 per kilobase in comparisons of Asians and Europeans (Schuster et al. 2010).

Further details of human migrational history are going to emerge, as new data are published and analysed. However, it is clear that Africa, and sub-Saharan Africa in particular, represents the human biodiversity hotspot; differences within Africans frequently exceed those between Africans and Eurasians (Yu et al. 2002). Going back to the question of why human racial groups proved so hard to identify genetically, there is little doubt that the demographic phenomena we could reconstruct have little to do with the long-term isolation, necessary for populations to diverge and form rather distinct gene pools.

6.4.4 Looking for the Main Human Groups

The statistical methods to describe population structure can be classed as either model-based (Pritchard et al. 2000; Corander et al. 2004; Tang et al. 2005) or model-free (Patterson et al. 2006; Reich et al. 2008). The most popular model-based clustering procedure, structure (Pritchard et al. 2000), assigns genotypes to an arbitrary number of clusters, k, attributing fractions of individual genotypes to different clusters, if necessary. Independent analyses are carried out for different k values, and results are compared across analyses. Conversely, model-free approaches do not make any prior assumptions about the demographic model under which populations evolved, and are often based on the transformation of a number of correlated allele frequencies in a smaller number of uncorrelated synthetic variables, or principal components (Patterson et al. 2006).

At least four model-based analyses of the global structure of the CEPH-HGDP populations have been published, based on different combinations of markers, starting from 377 STRs (Rosenberg et al. 2002) to 993 STRs (Rosenberg et al. 2005), 650,000 SNPs (Li et al. 2008), and 512,000 SNPs plus 396 CNV loci (Jakobsson et al. 2008). All these studies revealed the existence of geographical structuring at the continental level. Indeed, when forcing the number of clusters to be five, genotypes of the same population tended to occur together, in clusters approximately corresponding to continental subdivisions, namely Africa, Eurasia (i.e. the Middle-East together with Europe and Central/South Asia), East Asia, Oceania and the Americas (Rosenberg et al. 2002, 2005; Li et al. 2008). On the other hand, these studies differed as for the most likely number of clusters in the data, between 2 and 7, and for the distribution of genotypes in the clusters (compare Rosenberg et al. 2002 and Rosenberg et al. 2005). With $k = 6$, the sixth cluster identified an Asian isolate, the Kalash (Rosenberg et al. 2002), or led to separate two groups of American samples (Rosenberg et al. 2005), or to separate Central/South Asia from Europe and the Middle-East (Li et al. 2008). Despite the abundant evidence for an increased genetic diversity in Africa, all these studies assigned Africans to a single cluster, which seems rather puzzling. However, the presence of significant structure within Africa (as well as in the Americas), was detected in a reanalysis of the Rosenberg et al. (2002) dataset by a model-free method looking for geographical zones of increased genetic change (Barbujani and Belle 2006). There are many other examples, but here, the point is that clustering is always possible, but a general description of human population structure, largely independent of the markers and samples chosen, has not been achieved so far.

One way to further investigate population structure is to focus on restricted areas of the planet. When the Han Chinese population was compared with worldwide-distributed samples, in two studies of >150,000 SNPs (Xu et al. 2009; Chen et al. 2009), the result was a rather trivial separation of three continental clusters. It was only after removal of the non-Asian samples that differences between Japanese and Chinese, and especially a latitudinal gradient within Chinese, were identified (Fig. 6.2). Although nobody has located yet the lines separating the main human groups, there are many subtle discontinuities caused by various types of barriers, geographic as well as cultural, which are worth investigating.

6.4.5 Cultural Barriers and Genetic Diversity

When choosing a partner, humans do not tend to easily cross barriers, be they part of their physical or cultural environment. Therefore, populations separated by such barriers are somewhat reproductively isolated from each other. The genetic consequences may be substantial. In Europe, for instance, linguistic boundaries show increased rates of allele-frequency change (Sokal et al. 1988; Barbujani and Sokal 1990; Calafell and Bertranpetit 1994), and several inheritable diseases differ, in their incidence, between geographically close populations separated by language barriers (de la Chapelle 1993). But language differences have even greater evolutionary significance, because a common language frequently reflects a recent common origin, and a related language indicates a more remote common origin (Sokal 1988). Population admixture and linguistic assimilation should have weakened the correspondence between genetic and linguistic diversity. The fact that such patterns are, conversely, well correlated (Sokal 1988; Cavalli-Sforza et al. 1988; Chen et al. 1995; Nettle and Harriss 2003; Hunley and Long 2005; Hunley et al.

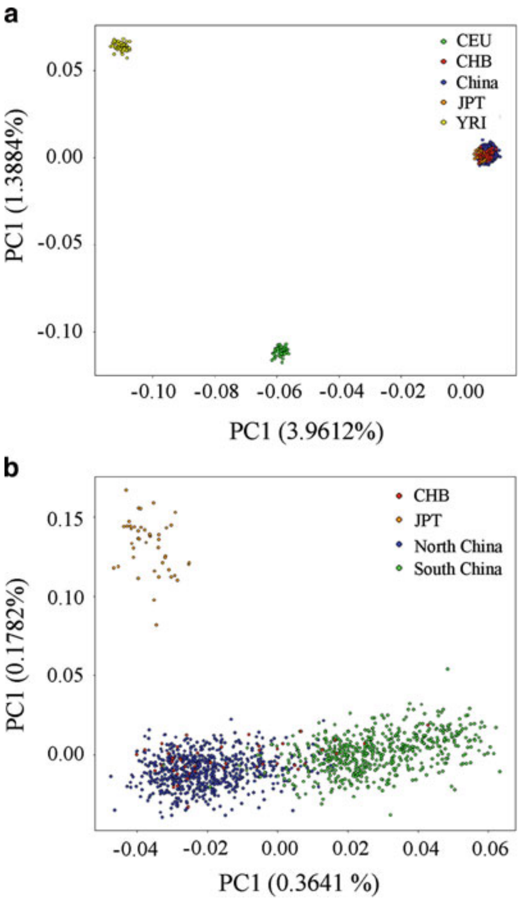

Fig. 6.2 (**a**) Two-dimensional plots based on the principal components (PC) 1 and 2 of Han Chinese (China) together with individuals from Africa (YRI), US residents with European ancestry (CEU), Japan (JPT) and Chinese from Beijing (CHB). The Asians clustered together. When the analysis is restricted to Asians (**b**) Japanese separate from Chinese and a north-south gradient appear within Han Chinese. Reproduced with permission and modified, from Chen et al. (2009)

2007; Belle and Barbujani 2007; Tishkoff et al. 2009; Heyer et al. 2009; Bryc et al. 2010) suggests that often genetic and linguistic changes occurred in parallel.

Many kinds of cultural barriers have left a mark in the distribution of human genome diversity; language differences are probably just more stable, and easier to study, than religious and political barriers which may also have important effects. India is a textbook example of how genetic stratification may arise in response to social barriers. Significant differences among populations seem to reflect, besides geography (Thanseem et al. 2006; Zerjal et al. 2007) and language (Indian Genome Variation Consortium 2008), the different levels of the caste system (Cordaux et al. 2004; Zerjal et al. 2007; Watkins et al. 2008; Reich et al. 2009). To have an idea of the power of these effects, in Tamil Nadu and Andhra Pradesh the differences between castes of the same region appear seven- to eightfold as large as the differences between members of the same caste, 500 km away (Watkins et al. 2008). Fragmentation along cultural, religious or social boundaries contributes to maintaining extensive variation within limited geographical areas.

6.5 How Did All This Come About?

Figure 6.3 is an attempt to assemble a coherent, if admittedly oversimplified, picture of human population history. Panel A represents the ancestral populations when anatomically modern humans were restricted to Africa, some 100,000 years

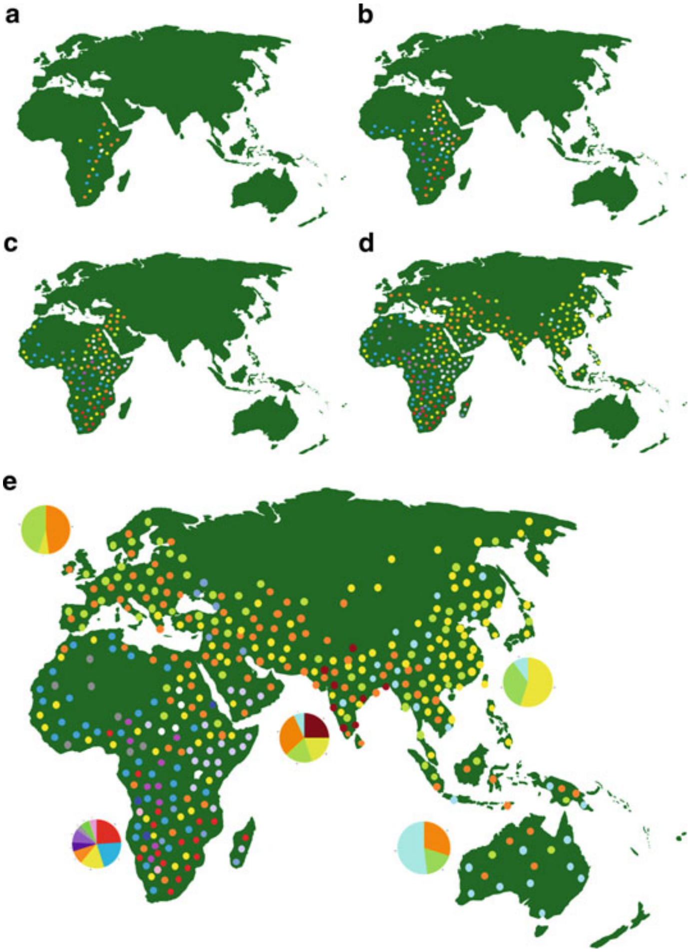

Fig. 6.3 A schematic view of the evolution of human biodiversity. *Dots* of different *colours* represent different genotypes. Approximate dates for the five panels (**a**, **b**) >60,000 years BP; (**c**) 60,000 years BP; (**d**) 40,000 years BP; (**e**) 30,000 years BP. A broader set of images is available at this site: http://web.unife.it/progetti/genetica/Guido/index.php?lng=it&p=11. Reproduced with permission, from Barbujani and Colonna (2010)

ago; the different colours represent different genotypes. The rest of the world was not devoid of humans; there were anatomically archaic people in Asia and Europe, but it is unlikely that they have contributed to the modern gene pool, and in any case that contribution must have been minimal (Foley 1998).

In panel B, we represent an expansion of the African population, which is accompanied by the generation of new alleles by mutation. Humans could not produce food at that time, and moved around looking for bearable living conditions. In the course of their movements, some of them reached north Africa, and in this scheme they were mostly carrying yellow and orange genotypes. When, around 60,000 years ago (Liu et al. 2006), these people crossed into Eurasia (here we did not represent a possible Southern route of dispersal in the Arab peninsula, through the horn of Africa: Macaulay et al. 2005), they entered a territory with greater resources and low population density (panel C). The main consequence was an improvement in living conditions, resulting in a demographic growth which, however, affected only the descendents of the people who left Africa, here represented by yellow, orange and green genotypes.

With time, the African emigrants' descendents came to colonise the planet, and all modern populations developed from these founders (panel D). Other mutations occurred, both in Africa and outside. However, at the end of the major expansion process (which was certainly accompanied and followed by other momentous demographic changes) the African alleles had dispersed worldwide (Watkins et al. 2001). The pie diagrams in panel E are meant to represent variation at a typical human locus, in which Africa shows a large number of alleles, both continent-specific and cosmopolitan. By contrast, each of the gene pools of the non-African populations is largely (although not exclusively) composed of a different subset of African alleles, sometimes brought to high frequencies by genetic drift. By effect of the repeated founder effects, the yellow genotype forms a West–East cline encompassing all Eurasia, with maximal frequencies in China.

We are aware that the synthesis we operated is brutal. Yet, if this model is just vaguely accurate, it explains why human alleles are basically either African or cosmopolitan; why so many indexes of genetic diversity are associated with distance from Africa; why human genetic diversity is largely clinal; and why it was, and still is, impossible to define natural clusters of human genotypes.

Future challenges include the study of complex traits, and the identification of the selective pressures that shaped variation at probably limited, but evolutionarily and clinically significant, portions of the genome. We suspect that insisting on the racial description of human biodiversity will not be very productive. Among Lewontin's critics, Edwards (2003) argued that by considering many loci at the same time one could discriminate among groups that overlap when studied at the single gene level (Witherspoon et al. 2007). In fact, the small variances observed between populations imply that any clustering will be based on small genetic differences, but do not mean that populations cannot be distinguished. However, the available evidence suggests that even when investigated for thousands of markers, the differences between populations and groups thereof are not only small, but also discordant across different genome regions (Li et al. 2008; Jakobsson et al. 2008). It seems fair to conclude that a stable description of human population structure, independent of the markers and samples chosen, has not emerged so far.

This may mean that we still need more markers, although recent analyses already exploited almost one million variable DNA sites. Alternatively, it may be that an elusive geographical structure, caused by the extensive genetic exchanges occurred in the species' history, is an important intrinsic feature of human biodiversity. Coming to terms with it may be an important starting point for a deeper understanding of the processes that generated our biodiversity.

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Part II
Biodiversity in the Palaearctic

Chapter 7
Mediterranean Peninsulas: The Evolution of Hotspots

Godfrey M. Hewitt

Abstract The Mediterranean peninsulas contain much genetic and species diversity, which decreases toward higher latitudes in Europe. In considering how such diversity evolved, three areas of activity seem important – Paleogeology, Paleoclimatology, and Phylogeography. The complex collision of the African and European tectonic plates produced the very different peninsulas of Iberia, Italy, and the Balkans. The climate cooled from 50 Mya with increasingly severe ice ages over the last 2 My that repeatedly modified species distributions and hence species evolution. As well as many endemic species, genetic methods show the peninsulas to have distinct genotypes in many species, with various postglacial histories. Their mountainous topography appears important for the survival of species through the ice ages and previously. In Iberia, mountains are the focus for multiple refugia, producing several diverged genetic lineages. Italy shows more recent subdivision through multiple refugia, particularly in the south. The Balkans has many more endemics, but fewer phylogeographic studies than other peninsulas. Multiple refugia and a range of lineage ages indicate continuous divergence and speciation over many millions of years to the present. The peninsulas are important as refugia for the survival of species and engines of speciation.

7.1 Introduction

The Mediterranean peninsulas of Iberia, Italy, and the Balkans contain much genetic and species diversity, with this generally decreasing toward higher latitudes in Europe. Throughout history and particularly recently they have been subject to

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increasing human pressures, so that their biotas are now greatly challenged and they are considered as important hotspots of biodiversity (Blondel and Aronson 1999; Myers et al. 2000; Mittermeier et al. 2003). Such deliberations usually rely on estimates of plant species diversity, since these are relatively well-known with some 25,000 species described in the Mediterranean basin. Well-studied vertebrates like reptiles show the same trend for southern species richness. But some groups like mammals do not; here the greatest species richness is found from the south of France across to southern Poland, probably as a reflection of the lifestyles that their homothermy allows. Invertebrates are much less well-studied, but highly speciose, with insects probably underestimated at some 150,000 Mediterranean species. They too generally follow the trend of higher diversity in the south of Europe; where, for example, recent studies indicate that the peninsulas are species rich for ants and longhorn beetles (Schlick-Steiner et al. 2008; Baselga 2008). However, species richness of butterflies although lowest in northern Europe, is highest in the Pyrenees, Alps, and Balkan mountains (Hawkins and Porter 2003), whereas the distribution for dragonflies is more similar to that for mammals (Keil et al. 2008).

There are a number of hypotheses for this general latitudinal cline in diversity (Currie et al. 2004) that derive from the fundamental increase in energy input from pole to equator and the distribution of habitats. The most favored of these argues that species richness is determined by the energy available for photosynthesis, where population density rises with more energy and thus extinction is lower. Another argues that speciation is higher in the tropics because metabolism, mutation, and reproduction are faster at higher temperatures. These models are essentially based on the contemporary Holocene climate, even those involving evolutionary aspects, and yet the climate has varied greatly through time, particularly over the last 2 My through the Pleistocene ice ages, causing major shifts in species distributions (Hewitt 1993, 2000). The genetic consequences of Quaternary climatic oscillations have begun to be explored in the last decade, particularly for Europe, North America, and Australia (Hewitt 1996, 2004a), and this indicates that for many species genetic diversity has been lost as species colonized out from glacial refugia. In Europe, this was largely northward from southern refugia. Furthermore these refugial regions have apparently harbored populations of species through many range expansions and contractions leading to their genetic divergence, accumulation of lineages, and speciation. Recently the effects of these major Quaternary fluctuations in climate have also been considered more fully in mainstream hypotheses for geographical variation in species richness, and support for them having a major role is growing (Dynesius and Jansson 2000; Montoya et al. 2007; Svenning et al. 2009). They may in part explain the latitudinal clines in diversity.

Thus the high genetic and species diversity found in the Mediterranean peninsulas is of considerable theoretic and conceptual importance, and it has great conservation value as recognized by their hotspot status. Understanding how such diversity evolved over time will allow for more informed decisions and actions. In considering this, three areas of recent activity and progress seem important – Paleogeology, Paleoclimatology, and Phylogeography.

7.2 Palaeogeology of Mediterranean Region

The collision of the African and European tectonic plates, with the subsequent complex structuring of the land and waters of the Mediterranean region from roughly the beginning of the Cenozoic (65 My), produced land bridges, sea straits, and ultimately the very different peninsulas of Iberia, Italy, and the Balkans (Fig. 7.1).

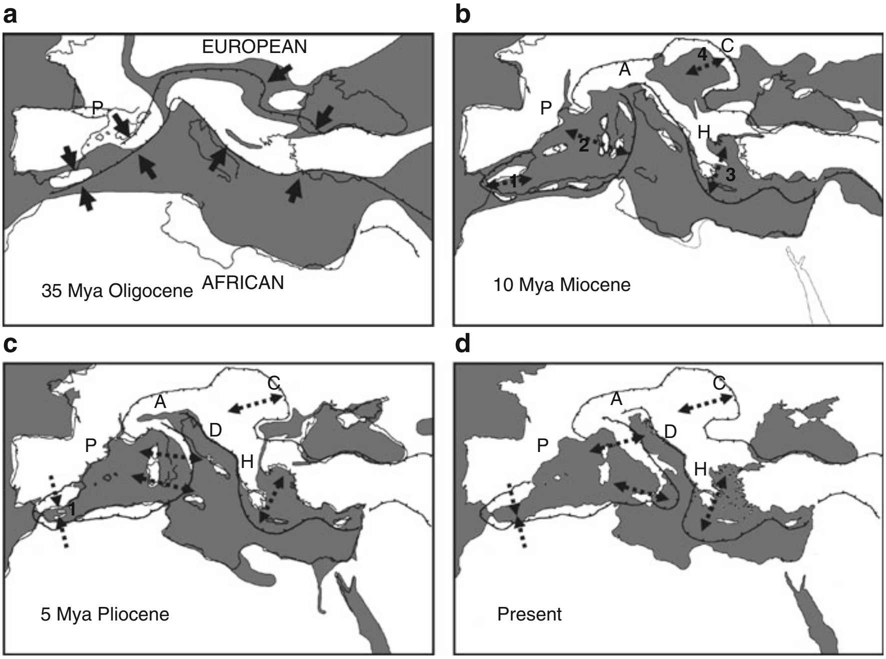

Fig. 7.1 *The geological evolution of Mediterranean Peninsulas*. The thrusting of the African and European tectonic plates from the Oligocene to the present indicating major faults, subduction and orogeny. An indication of probable land form and sea extent is shown (modified from Carminati and Doglioni 2005; Jolivet et al. 2006). (**a**) The Oligocene shows the Fore- and Retro-belts of subduction between the colliding plates, with the Pyrenees (P) largely formed, and with only very early Alpine and Hellenic orogeny. (**b**) The Miocene shows well advanced Alpine (A) and Hellenic (H) orogeny, with Carpathian (C) orogeny proceeding. There is activity in the Betic-Rif region (1), the Apennines front has migrated eastwards from Iberia taking proto-Sardinia and Corsica (2), the Dinaric-Hellenic Forebelt has bulged south-eastwards (3), and the Carpathian front has migrated north-eastwards (4). (**c**) There is further activity and migration in all the four regions noted in the Miocene, and this shows the Mediterranean Sea refilled after the Messinian Crisis when it largely dried up. The Alps, Dinaric (D) ands Pindus (H) mountains are well established. The Atlas orogeny proceeds and the Betic-Rif region (1) consolidates. The retraction of relic Tethys waters to the Black Sea opens proto-Balkans to the north. (**d**) The Present shows further movements and orogeny with the completion of the Italian Peninsula, and aggregation of Sicily in the Pleistocene. The Black Sea waters have contracted further

The leading edge of the African plate subducted under the European plate breaking the edge into smaller microplates and land masses that moved in various directions (Robertson and Grasso 1995; Carminati and Doglioni 2005; Jolivet et al. 2006). The details of this tortuous and convoluted process are still much debated and researched, but certain points seem particularly relevant for the evolution of the peninsular biotas. From its first formation in the late Eocene, the Mediterranean Sea was open to the Atlantic, being cut off from the old Tethys Sea to the east. The Iberian land mass is ancient and the Pyrenees arose early, their uplift culminating in the Eocene. At this time there was significant Balkan and Hellenic orogeny, with several ridges and submerged channels, and continuity with proto-Turkey. However, the Alps were only just beginning to form as the submerged Apulian plate thrust into Europe, with their orogeny climaxing in the Miocene (~20 My). The Italian peninsula formed much later as a composite of Iberian, African, and Hellenic components.

A number of other relevant changes occurred during the Oligocene and Miocene (~34–6 My). In the west, sections of the Iberian plate swung across to the Apennines, leaving Corsica, Sardinia, and the Balearic Islands in between. The Sierra Nevada and Atlas ranges were forming, with the Betic-Rif land masses moving about between Iberia and Africa (30–10 My) (Rosenbaum et al. 2002). Through this time, Greece and the Balkans were largely connected to Turkey and it in turn with Arabia (and hence ultimately Africa) and the Zargos and Caucasus Mountains to the east. At the end of the Miocene (~6 My), the drift of Africa toward Europe closed the western end of the Mediterranean, and without the influx of Atlantic waters the basin largely dried up. This Messinian Salinity Crisis (5.6–5.3 My), produced land connections between North Africa and Europe, through both Iberia and components of proto-Italy. The Mediterranean refilled around 5.33 My ago with the opening of the Straits of Gibraltar, which have not been closed since (Duggen et al. 2003). With the filling of the Aegean Sea and the large but reduced Black Sea to the north, Turkey became semi-detached from Greece and the Balkans, and the rest of Europe. The Adriatic was large, continuing well up the Po valley, and the various bits of Italy came together later in the Pliocene. Indeed the several components of Calabria and Sicily have been uplifting and joining in the Pleistocene (2 My) (Bonfiglio et al. 2002). The Iberian, Balkan, and Italian peninsulas thus have different origins, ages, connections, and components, and these factors need to be considered when thinking about the evolution of their biota, be it individual species or whole groups.

7.3 Palaeoclimate Through the Cenozoic

The Cenozoic began with the K-T extinction event (65 My) when the number of species was reduced drastically by perhaps 85%, with some groups faring worse than others. Since then species richness has been increasing rapidly, particularly in

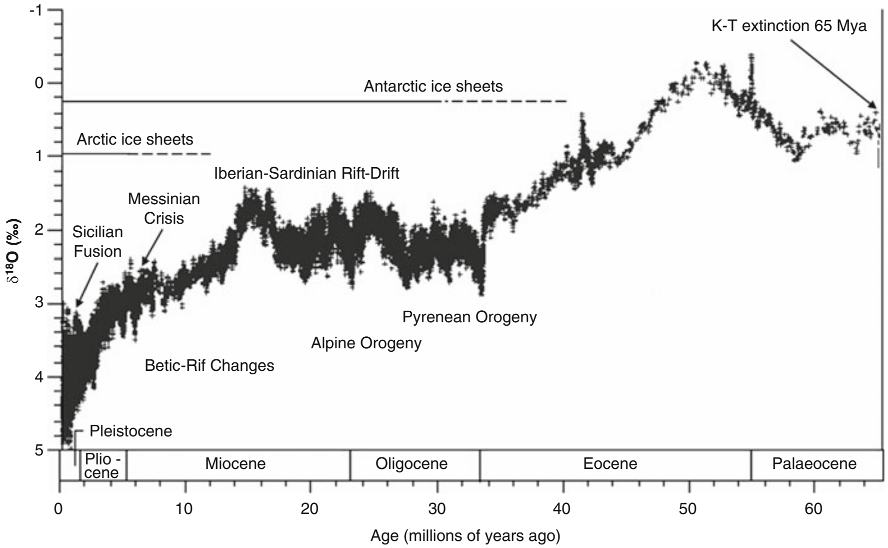

Fig. 7.2 *A time course of Mediterranean geological events and climate through the Cenozoic*. The climate cooled through the Cenozoic (as measured by Oxygen isotope changes – modified from Zachos et al. 2008) with growth of Antarctic and Arctic ice sheets. Relevant events of mountain orogeny, land drift and fusion are indicated (see text)

marine and terrestrial animals and is now higher than ever before. Recent work indicates that the global climate warmed until the early Eocene (50 My) and since then has been cooling, with some perturbations (Zachos et al. 2008) (Fig. 7.2). This involved the formation and growth of Antarctic ice sheets from the late Eocene (35 My), and following the mid-Miocene climatic optimum (10 My), Arctic ice sheets grew from late Miocene (7 My). These latter became continuous and extensive in the Pleistocene (2 My), which produced increasingly severe ice ages that greatly modified species distributions many times (Hewitt 1993, 2000). These major ice ages latterly (0.9 My) have a 100 ky periodicity that is driven by the eccentricity of the earth's orbit around the sun, one of the three Milankovitch cycles. In the earlier Pleistocene and back into the Pliocene, they were less severe and had a 41 ky periodicity that reflects the obliquity of the earth's axis. Both the degree of eccentricity and obliquity, along with that of the axis precession (23/19 ky cycle) affect the insolation of the earth, and hence its climate. Such orbital oscillations are fundamental and will have affected climate back through time, with their effects transferred by ocean conveyors and modified by plate tectonic changes. We know increasingly more about the Quaternary period (last 2 My) from advances in palaeoclimatology and palaeobiology, and there are some interesting data and deductions about earlier periods. But more such study should be encouraged in order to better understand the earlier evolution of species and biotas.

7.4 Quaternary Europe Species Ranges

Climate has been cooling through the Quaternary with marked oscillations, and we have had some ten major ice ages with warm interglacials in the last 1 My. Within these major cycles there have been many rapid changes of hundreds to a few thousand years, so called millennial oscillations, that have been determined from ice cores particularly and that can show great temperature amplitude. The extent of glaciation varied somewhat with each ice age, and during the last glacial maximum (LGM, 25–18 ky) Europe was covered with ice down to Norwich and Warsaw. South of that was permafrost, tundra, and steppe. Europe has an excellent fossil record from pollen, beetles, and bones and these show that during the glacial maxima, species ranges contracted to southern parts, particularly the peninsulas, from which they expanded postglacially to their present interglacial ranges (Bennett 1997; Williams et al. 1998; Hewitt 2000).

Conditions for most of today's European species were at their worst during the LGM and their ranges consequently maximally restricted. Just where these refugial populations were in southern Europe depends on each species' individual adaptations and niche, and the distribution of their habitat. Species with more temperate adaptations would have refugial ranges further south in general than those more cold-hardy, whereas present day Arctic/Boreal species would have survived closer to the ice (Hewitt 2004a, b). For example in small mammals, species with southern and northern temperate species ranges might be the wood mouse, *Apodemus sylvaticus* (Michaux et al. 2003) and the field vole, *Microtus agrestis* (Jaarola and Searle 2002). Present day Alpine species probably had broader distributions in nonglaciated regions around the mountains and beyond during such cold periods (Schmitt and Hewitt 2004b). Clearly a good fossil record is important in accurately determining the limits of refugial ranges with confidence, and sufficiently detailed ones are not available (or even possible) for many species. The network of pollen cores across Europe provides some of the best evidence for reconstructing the distribution and movement of plant species, and hence the vegetation changes through the ice age and after. This indicates that key temperate species, like the oak, were present in the peninsulas during the LGM. But even these, our best data, have problems of detail, in that in most cases they do not absolutely prove that the species was present all the time in a particular location or region. This can only be shown by analysis of serial-dated sections through the LGM, as done for oak in Greece (Tzedakis et al. 2002, 2004). Given the repeated and relatively severe climatic oscillations on the centennial–millennial scale during the ice age, including in the LGM itself, it seems likely that populations in refugial regions experienced considerable demographic changes, with many blinking on and off. Many fossils of different ages from an area are needed to locate refugial regions with confidence.

Recent detailed analysis of fossils that emphasizes accurate dating of the bones of several mammal species through the last ice age shows how their ranges changed, and particularly where they were during the LGM. Sufficient numbers of specimens were available for bears, hedgehogs, red deer, and roe deer (Sommer and Benecke 2005; Sommer 2007; Sommer et al. 2008, 2009) to allow fairly confident conclusions on the species' major range changes in this time. For the bears, fossils have so far been found only in Iberia and Moldovia during the LGM, while for hedgehogs LGM fossils are in Iberia, Italy, and the Balkans. Interestingly, this careful temporal analysis of the fossil record also shows that the bears colonized northern Europe rapidly after the LGM in the warm Greenland Interstadial (12.5–11 ky), whereas hedgehogs were much slower and mainly after the Younger Dryas cold spell (11–10 ky). Red deer and roe deer were found in the peninsulas and also southern France and Carpathians during the LGM, with the postglacial expansion of the roe deer being more affected by the Younger Dryas. Such spatially extensive and temporally accurate fossil data is needed for other species, and is particularly valuable when combined with equally extensive and well-analyzed genetic data, as may be seen in the above four examples.

The ranges of species across Europe would have contracted and expanded with each major ice age and also with millennial oscillations, like the Younger Dryas, within each ice age. Many species could respond quite rapidly, with the extent of range change depending on the severity of the change in climate. Such repeated range changes are an important feature of species evolution and are responsible for moving and molding their genomes. Indeed this repeated demographic and geographic contraction and expansion is the norm, the shifting stage on which processes of selection, adaptation, divergence, speciation, and extinction occur, and is likely to affect genetic diversity today.

7.5 Phylogeography of Europe

In the last 2 decades, there have been great advances in genetic methods for sequencing DNA and for describing and analyzing genetic variation and diversity and this continues apace. They allow us to deduce genetic relationships in space and time (Hewitt 2001). The field of Phylogeography, which seeks to understand the causes of the geographical distribution of genealogical lineages, has burgeoned since the advent of the polymerase chain reaction. This provides the ready ability to determine chosen DNA sequences across an organism's range and deduce their history from the divergences they show. There has been an explosive growth of the field (Avise 2009), and the number of publications is still accelerating. Web of Science records 4,217 papers since 1987 under search for "Phylogeography." Of these 678 cited "Europe," and of these 32 Greece, 53 Balkans, 81 Italy, 41 Iberia, 60 Spain, and 16 Portugal, with 268 citing "Refugia". By 1998 – half-way to today from the naming of the field in 1987 – there were just 23 for Europe (Comes and Kadereit 1998; Taberlet et al. 1998; Hewitt 1998)! This earlier work necessarily concerned few species, but pointed the way in describing postglacial colonization routes for distinct genetic lineages from southern Europe to the north. It indicated the importance of southern refugia and the Mediterranean peninsulas in particular.

Since then many more species have been analyzed in detail – from the Arctic to North Africa – with latterly a growing interest in Mediterranean regions.

Postglacial colonization routes from southern refugia have been deduced from genetic data for many species and a variety of patterns are revealed (Hewitt 2004a; Schmitt 2007). Those of the grasshopper, bear, hedgehog, chub, and marbled white are considered as exemplars of distinct patterns with northward colonization involving different combinations of refugia. Considerable genetic divergence is found for most organisms among the peninsulas and often with regions to the east including Turkey and the old Soviet Union. These refugial regions contributed differently to the colonization of Europe for different species, with Balkan lineages predominating in many of them, Iberia in a moderate number, and Italy in rather few. This is probably due to the major mountain barrier to postglacial colonization posed by the glaciated Alps and lesser one by the Pyrenees up to the Younger Dryas and Holocene period. The lineages carried by such retarded organismal migrations met those from other refugia that had expanded and filled the space, often with the formation of hybrid zones (Hewitt 1996, 1998). The colonization of northern European regions by species with lineages from different refugia has produced very mixed biotas (Hewitt 2004a, b). For example, the UK has meadow grasshoppers from the Balkans, hedgehogs and oaks from Iberia, and chub from the Black Sea via the Danube; whereas Scandinavia has its grasshoppers from the Balkans, hedgehogs from northern Italy, bears from Iberia and near the Caucasus, and chub from a different Black Sea refugium via Russian rivers. This discovery has significant implications for understanding adaptation, competition, coadaptation, the rate of evolution, speciation, and conservation. It emphasizes the importance of the peninsulas in preserving diversity and particularizes their contribution to recolonizing the rest of Europe.

The extent of DNA divergence between lineages from different refugial regions including the peninsulas varies, and is quite large for several species or sister species. For example, the hedgehog (*Erinaceus concolor*) from the Balkans is perhaps some 4 My diverged from Iberian and Italian stock (*E. europaeus*), whereas the latter two are some 2 My apart (Seddon et al. 2001). Other species with such Pliocene divergence are the toad *Bombina*, the newt *Triturus*, and the snake *Natrix*. Many other species have peninsular divergences that would date from various times in the Pleistocene, with some probably only one or two ice ages old (Table 7.1). Such divergence is explained by species surviving in the southern refugia over a number of ice ages and diverging. With each warming period some populations would expand and colonize parts of Europe to the north, and with each cooling these expansions would go extinct – the extent depending on the degree of climate change. The southern parts of Europe including the peninsulas are mountainous and the varied topography would have provided varied and suitable habitats for the species to survive climatic oscillations by locally tracking their habitat (Hewitt 1996). Mountain regions in other parts of the world seem likely to serve a similar function in preserving and generating diversity (Fjeldsa and Lovett 1997).

The earlier European phylogeographies also indicated considerable lineage diversity within the peninsulas in several species, and suggested that with more

Table 7.1 Genetic Age of Divergence among Mediterranean Peninsular Refugia for Widespread Species

Organism	Genetic markers	Divergence Age	Refugia	Recent Reference
Cervus elaphus	Mt-cytb/Dlp	1.4% 100 ky	S B	Skog et al. (2009)
Myotis myotis	Mt-Dlp/STRs	2.2% 110 ky	S (I) (B)	Ruedi et al. (2008)
Lepus europaeus	Mt-Dlp	239 ky 128 ky	? I (B) T	Fickel et al. (2008)
Cinclus cinclus	Mt-cytb/ND/CR	46–280 ky <3.8%	(Af) S/I B R*	Hourlay et al. (2008)
Sorex araneus spp	Mt-cytbCO1/Y	0.1–2 My	S (I) B Ca	Yannic et al. (2008)
Melitaea cinxia	Mt-CO1	2–6% 1–3 My	(Af)S B As	Wahlberg and Saccheri (2007)
Emys orbicularis	Mt-cytb	~1% 1–5 My	S* I*B*BS. (Cas)	Fritz et al. (2005)
Strix aluco	Mt-CR2/ms	0.3–0.4 My	(S) (I) B	Brito (2007)
Capreolus capreolus	Mt-CR/ms	45–200 ky	S* (I) B	Royo et al. (2007)
Bombina bombina spp	Mt-cytb 1096bp	8–11% 1–5 My	I B Ca BS	Hofman et al. (2007)
Natrix maura/ tessellata	Mt-cytb/ncISSR	18% ~18 My >2 My	(Af)S*? B*Cas*As	Joger et al. (2007)
Crocidura suaveolens	Mt-cytb/nc 1797bp	0.06–1.7 My	S IB T As	Dubey et al. (2006)
Ursus arctos	Mt-CR, fossils	3–7% 0.3–0.8 My	S (I) B Ca	Sommer and Benecke (2005)
Apodemus sylvaticus	Mt-cytb	1.5 My	(Af) S (IB)	Michaux et al. 2005
Apodemus flavicollis	Mt-cytb	0.4 My	B R (T)	Michaux et al. (2005)
Triturus vulgaris ssp	Mt-1800 bp	1.0–4.5 My	(I) B* Ca (T)	Babik et al. (2005)
Microtus agrestis	Mt-cytb	0.53% 50–83 ky	S I B Ca R	Jaarola and Searle (2002)
Erinaceus europaeus spp	Mt-cytb	6–12% 3–6 My	S* I* B* (T)	Seddon et al. (2002)
Arvicola terrestris	Mt-cytb	4–7.6% 2–4 My	S I B	Taberlet et al. (1998)
Chorthippus parallelus	Mt 6.7 kb/nc	0.8% 0.3–0.5My	(S*) (I) B* (T)	Szymura et al. (1996)

Some show ancient divergences, but many are recent – a few ice ages or in the Pleistocene. Probable LGM refugia are Af (Africa), S (Iberia), I (Italy), B (Balkan Peninsula), T (Turkey), Ca (Carpathians), BS (Black Sea), Cas (Caspian), R (Russia – Caucasus to Urals), As (Asia – East of Urals). *Underlined* refugia, S or B provided the major northern colonization, while refugia in parentheses, (Af) (S) (I) (B) (T) did not apparently expand from the area. Refugia marked * show evidence of multiple refugia, which also probably exist elsewhere

extensive sampling this might be shown to be a major widespread feature (Hewitt 1998). For example, DNA data from the meadow grasshopper *Chorthippus parallelus* indicated several separate refugia within Iberia and other peninsulas, but was not able to locate these more precisely (Hewitt 1996). The hedgehog postglacial colonization of Europe involved several distinct lineages from each peninsula, arguing for several separate refugia within each (Santucci et al. 1998;

Seddon et al. 2001). Turkey also contains several lineages and therefore refugia, but did not contribute to the recent European repopulation (Seddon et al. 2002). Since such earlier suggestions of multiple refugia in southern Europe and within the peninsulas there has been increased phylogeographic effort to illuminate this significant biogeographic pattern. This has been most apparent in Iberia, and the three Mediterranean peninsulas will be examined in turn.

7.6 Iberia: Refugia Within Refugia

The mountainous topography of Southern Europe appears important for the survival of species through the ice ages, and previously in the Caenozoic following the formation of individual ranges. We may envisage that populations would ascend and descend, move up valleys and over ridges, onto nearby lowland and back, tracking their shifting suitable habitat as temperature and humidity oscillated. This would be possible within each dissected mountain block or local range. In Iberia this structure with several mountain ranges is seen as the framework for multiple refugia, producing several diverged genetic lineages. Many cases of species with distinct geographic genetic lineages have been revealed recently across a range of animal and plant groups, with several fine examples in amphibians and reptiles. An excellent review (Gomez and Lunt 2007) collated and summarized this emerging information, and more papers have appeared since (e.g., Paulo et al. 2008; Pinho et al. 2007a, b; 2008; Pico et al. 2008; Terrab et al. 2008; Guicking et al. 2008; Santos et al. 2008, Lopez de Heredia et al. 2007; Rodriguez-Munoz et al. 2007; Bella et al. 2007; Royo et al. 2007; Martinez-Solano et al. 2006; Rowe et al. 2006; Kutnik et al. 2004; Michaux et al. 2003; Ibanez et al. 2006; Ortego et al. 2009). This reveals that over 60 species have genetic lineage divergence indicating 2 or more putative refugia within Iberia. Further possible examples exist in foxes, shrews, snails, water voles, *Pinus, Frangula,* and other species, and we can expect many more.

From these phylogeographic data there are regions where several species each have a distinct local lineage, and such phylogeographic concordance indicates it as a refugial region. There are seven main refugial areas recognized in Iberia for largely terrestrial species (see map Gomez and Lunt 2007), the Betic ranges in the south, Serra da Estrela in the west, Portugal north of the Mondego River, the Picos de Europa, the Systema Central, the Pyrenees, and the Ebro Valley. These are also regions of high-species endemism, as would be expected of long-term refugia that allowed the survival and divergence of separate lineages to produce species. These regions harbor many different species and a range of types of organism, which means that a suitable range of habitats have probably existed somewhere within them for millions of years and over many climatic changes. As mentioned, there are many phylogeographic publications, but to illustrate the main points this article will necessarily concentrate on some species that are well-sampled and have detailed DNA sequence data. Others often support the conclusions.

Considering amphibians and reptiles, these vary somewhat in their habitats from more to less dependence on humidity, they are a feature of the Iberian biota and a number of phylogeographies for species complexes have become available recently. Interestingly these reveal the Betic ranges, Portugal, and the Systema Central as common refugia and likely the theatre for much Pliocene and Pleistocene evolution. The relatively high humidity of the Atlantic coast now and during the ice ages would have favored species such as *Discoglossus galganoi*, *Chioglossa lusitanica,* and even *Lacerta schreiberi*, whereas *Salamandra salamandra* is capable of a somewhat wider expansion, and more xeric lizards like *Lacerta lepida* and *Podarcis hispanica s.l.* occupy all Iberia and into southern France and North Africa. Fish have rather different habitat requirements from terrestrial animals, and perhaps not surprisingly they show different refugial areas, with separate phylogeographic lineages for the main river catchments; major ones like the Duero, Tago, Mira, Adade, Guardiana, Guadalquivir, Ebro, Jucar, and several others are identified by Gomez and Lunt (2007).

The phylogeographic data now becoming available for some species, particularly as noted for amphibians and reptiles, allows us to address some more detailed and intricate problems of refugial formation and functioning. While due care needs to be taken when seeking to use the DNA divergence between lineages to date their separation, the better phylogenies show reasonably clearly that several lineages have diverged millions of years ago in the Pliocene or even Miocene. The shallower parts of the trees shed light on the phylogeography through the Pleistocene and ice ages, with the present-day distribution of genetic variation providing most insight into the last ice age and postglacial events. Thus many species show some evidence of postglacial population expansion from refugia, in the extent of the geographic range of some clades and in their genetic diversity, phylogenies, and haplotype networks. This is very clearly seen in studies on the following amphibians and lizards *Chioglossa lusitanica* (Alexandrino et al. 2007; Sequeira et al. 2008), *Lacerta schreiberi* (Paulo et al. 2001; Godinho et al. 2008), *Salamandra salamandra* (Steinfartz et al. 2000; Garcia-Paris et al. 2003), *Discoglossus galganoi*, *D.jeanneae* (Garcia-Paris and Jockusch 1999; Gomez and Lunt 2007), *Lacerta lepida* (Paulo et al. 2008) and *Podarcis hispanica* (Pinho et al. 2008). In particular, the expansions northward into NW Iberia of clades from refugia in northern Portugal and of other clades across Iberia to the north east from southern and western refugia are well-demonstrated. Detailed genetic data can allow a more precise location of glacial refugia for individual clades, particularly when combined with fossil and pollen data, and modeling of climatically induced range changes. Thus, from present data the valleys of the Douro, Mondego, and Tagus rivers in Portugal are indicated as likely candidates for several western-based clades and species.

As such diverged Iberian clades expand postglacially from their separate refugia they are likely to form hybrid zones on contact, as seen for expansions to northern Europe (Hewitt 1988, 1998). With multiple refugia this will produce a patchwork of parapatric clades in each species, as seen in many species and particularly so in *Lacerta lepida* and *Podarcis hispanica s.l.* When two clades have diverged genetically for some time the hybrids between them will generally show considerable unfitness, and this will produce narrower hybrid zones than contacts between more recently diverged clades. Hybridization between two younger clades is more likely to produce introgression and allele transfer than narrow hybrid zones between older diverged lineages. Some lineages show divergence indicative of considerable age, through the Pleistocene and into the Pliocene and this implies that some refugia have harbored lineages over these long periods. It seems possible therefore that contractions and expansions of recent ice ages have been broadly similar producing hybrid zones repeatedly and often in the same regions. Earlier in the evolution of the species when the deeper lineage divergences were occurring, the distribution and range shifts of older clades would necessarily have been different; the genetic structure of the species would have developed as environmental conditions changed with some clades going extinct and others expanding, particularly with major climatic fluctuations.

Evidence for such events has recently been provided in the Iberian emerald lizard *Lacerta schreiberi* (Godinho et al. 2008). Using a suite of mitochondrial and nuclear markers, the authors deduce some of the history of clade divergence and range changes from the Pliocene. In particular a narrow mtDNA hybrid zone in the Systema Central near Malcata has wide introgression of nuclear markers, which indicates several contacts and exchange of alleles through the recent ice ages. From a study of hybrid zones in *Salamandra salamandra* there is also evidence for repeated range shifts and differing genetic admixture (Garcia-Paris et al. 2003). The geographic distribution of related clades relative to more anciently diverged ones can suggest where and when these vicariances occurred and possible older refugia. The distribution of clades in *L. schreiberi* (Paulo et al. 2002; Godinho et al. 2008) indicates early vicariance of coastal and inland lineages, followed by separation of the southern isolated lineages that possibly have survived Pleistocene climatic changes through local altitudinal shifts. In *S. salamandra* (Steinfartz et al. 2000) the geographic distribution of clades shows “orphan” lineages in Northern Spain and Southern Italy, these are isolates of an older lineage expansion that have been surrounded by expansion of another lineage following the last ice age, clearly demonstrating some of the possible phylogeographic complexity produced by repeated range changes. It is exciting that we are beginning to find evidence to illuminate such biogeographic evolution, but also salutary to realize that much-detailed geographic sampling and composite genetic data are required to do this properly.

7.7 Europe to Africa: And Back Again

North West Africa was apparently first joined by land with Southern Iberia about 6 Mya as the two crustal plates pushed further into each other. This enclosure of the Mediterranean Sea lead to the Messinian Salinity Crisis, when it largely dried out leaving saline lakes and flats. This is seen as providing routes of exchange for terrestrial organisms, although these may have been limited given the aridity and salinity of the region. Routes seem most likely between present-day Morocco and Iberia and Tunisia and Italy. At 5.33 Mya the Atlantic broke through the Straits of Gibraltar and flooded the Mediterranean completely over perhaps a century; these straits have not been closed since, but were narrower with lower sea levels in glacial maxima. There is much interest in applying genetic methods to investigate the extent and timing of biotic exchange between Europe and Africa and, although there is genetic evidence for both Iberian and Italian routes from Africa (Habel et al. 2008; Skog et al. 2009), many more studies concern the role that the Straits of Gibraltar played in the structuring of the Iberian biota.

A number of groups contain distinct species in North Africa and Iberia, indicating that the Straits of Gibraltar have been an effective barrier to genetic exchange and hence allowed the divergence of populations to become species. Indeed it is considered a greater biogeographic barrier than the Alps or Pyrenees. The Messinian Crisis with the land connection that accompanied it is often seen as the major period for exchanges of organisms between Africa and Europe, so deliberations and calculations on the form and rate of divergence and speciation tend to use the date of its termination by Atlantic flooding (5.33 Mya) as a strong timing point in phylogenies and trees. However, some recent studies provide growing phylogenetic evidence for more ancient and for modern crossing of the Straits of Gibraltar.

Several species show little or no genetic divergence across the Straits, and so some effective crossings probably occurred during or after the last glaciation and some more recently still with human assistance. These include larks (Guillaumet et al. 2006), shrews (Brandli et al. 2005), tortoises (Alvarez et al. 2000), snakes (Carranza et al. 2004, 2006b), chameleons (Paulo et al. 2002), lizards (Harris et al. 2002), salamanders (Veith et al. 2004), and frogs (Recuero et al. 2007). Some lizards (Carranza et al. 2006a) and terrapins (Fritz et al. 2006) have low genetic divergence indicating crossing during the Pleistocene, possibly with lower sea levels in the glacial maxima. Other species show higher DNA divergences that may be dated from the Pliocene and even the Late Miocene, and those dated around 5–6 Mya may be associated with the Messinian Crisis – viz: *Natrix maura* (Guicking et al. 2008), *Podarcis hispanica* (Pinho et al. 2007a, b), *Pleurodeles watl* (Veith et al. 2004). However, there are high divergences in the salamander *Pleurodeles watl* (Veith et al. 2004), and lizards *Podarcis hispanica* (Pinho et al. 2006), and *Lacerta lepida* (Paulo et al. 2008) that indicate earlier crossing between 7 and 14 Mya. Even with the problems of calibrating molecular clocks, this would be well before the Messinian land connection between Africa and Iberia. These latter two studies are particularly informative, with the first revealing that lineages were established by crossings in both directions between North Africa and Iberia, and the second that lineage divergence in this region may have been driven by the tectonic activity of Betic and Rifian orogeny in the Late Miocene and Early Pliocene. Such events may well have occurred in other species.

A recent study compared the mitochondrial and nuclear divergences among populations of 18 species of bat that occur on both sides of the Straits of Gibraltar (Garcia-Mudarra et al. 2009). Some six of these had very little difference between

African and Iberian representatives with less than 1% maximum mtDNA divergence, five had maximum divergence between 1 and 2%, and 7 had over 5% divergence – with the highest *Plecotus austriacus* at 14%. This clearly supports colonization and vicariance occurring throughout the Pliocene and Pleistocene – from some 7 Mya to the present. Interestingly there was no correlation with the dispersal ability as measured by wing aspect and loading, but one might expect the chance of colonization across the Straits of Gibraltar to be greater for more mobile species, and a number of volant species have phylogenies that indicate that the Straits have not been a complete barrier to dispersal (Hewitt 2004b). Clearly for these bats, and probably other groups, this must depend on other factors.

The Iberian Peninsula contains diverged lineages within species indicating multiple geographic refugia, and the data we have from various North African taxa indicate deep divergence among some regions, particularly between Tunisian and Moroccan lineages in reptiles (Barata et al. 2008). Clearly more study is needed of this region's phylogeography and systematics; it is adjacent to the Iberian Peninsula, is also part of the Mediterranean hotspot complex and has also been affected by crustal tectonics and ice age cycles. It appears that there have been occasional successful migrations back and forth between Africa and Iberia from the Mid-Miocene and these will have enriched the diversity of both regions. Because of the problems of dating molecular divergences, care should be exercised in ascribing cause for divergence to the relatively short Messinian event. Much more comparative phylogeography, hopefully combined with fossil data, is needed to develop a stronger understanding of exchange and divergence between Africa and Iberia. It would seem that rafting across narrow waters is possible, and that the Pre-Messinian uplift between Africa and Iberia closing Betic and Rifian channels deserves more study; it may well have allowed earlier opportunities for exchange and divergence in the Late Miocene.

7.8 The Italian Peninsula: A Younger Conglomeration

As noted previously, the Italian Peninsula formed much later than Iberia as a composite of Iberian, African, and Hellenic components, with its present form emerging very recently. Through about 34–6 Mya sections of the Iberian plate swung across to the Apennines, leaving Corsica, Sardinia, and the Balearic Islands in between. The emergent northern Appenines connected with the Alps in the mid-Pliocene, and the several bits of Italy came together late in the Pliocene, with parts of Calabria and Sicily joining in the Pleistocene (2 My) (Bonfiglio et al. 2002). We might expect this formation to produce a rather different genetic history and distribution of lineages. There are fewer phylogeographic publications for Italy than Iberia, but early work used the separation of Corsica–Sardinia from the Pyrenees at 29 Mya and the separation of Corsica from Sardinia around 9 Mya to examine molecular clocks in taxa that had diverged in these disjoining terrestrial locations, in particular newts and salamanders (Caccone et al. 1997). A number of the taxa studied in Iberia, like *Lacerta lepida s.l., Podarcis hispanica s.l., Discoglossus spp, Triturus spp,* and *Natrix spp*, most probably contain clades and forms diverging in the Pliocene and Pleistocene, and this seems likely for other species where the genetic data is not so clear yet. Similar Italian taxa contain divergences from the Pleistocene only, which could be due to the young age of much of the peninsula. Of course fewer Italian taxa have been examined in detail phylogeographically and more are needed to test this. Also it would be interesting to compare the genetic structure of taxa that inhabit the components of the peninsula that have Iberian, African, and Hellenic origins. However, it may be that the post-Messinian inundation cleared the signals of African and European colonization that may have occurred earlier.

Now there is growing genetic evidence for recent subdivision through multiple refugia. Some 21 species show clear genetic evidence of several glacial refugia, and it is likely that many more will appear when sufficient detailed genetic data is produced. Clear examples are seen in plants and vertebrates such as *Lepus, Capreolus, Talpa, Erinaceus, Cinclus, Hierophis, Podarcis, Vipera, Emys, Lacerta, Chalcides, Bombina, Salamandra, Rana, Heligmosomoides, Fagus, Fraxinus* (Fickel et al. 2008; Vernesi et al. 2002; Ungaro et al. 2001; Seddon et al. 2001; Hourlay et al. 2008; Joger et al. 2007; Podnar et al. 2005; Ursenbacher et al. 2006; Fritz et al. 2005; Bohme et al. 2007; Giovannotti et al. 2007; Canestrelli et al. 2006, 2008; Steinfartz et al. 2000; ; Nieberding et al. 2005; Vettori et al. 2004; Heuertz et al. 2006). Once again it is detailed sampling with mtDNA sequence and nuclear markers in amphibians and reptiles that provides the best evidence and examples. Many of these species show northern, central, and southern genetic components that may be related to major mountain blocks. The distributions are particularly dissected in the south, as nicely exemplified by the phylogeographies of *Hyla intermedia, Rana lessonae, Rana italica,* and *Bombina pachypus* (Canestrelli et al. 2006, 2008; Canestrelli and Nascetti 2008). Many of these clades are associated with mountains that were emergent islands progressively joined through the Pleistocene, but then separated by high sea levels in earlier interglacials in places like the Volturo River, Crati-Sibiri Plain, Cantanzaro Plain, and Straits of Messina (Fig. 7.3). This produces some clustering of contacts and hybrid zones, and so indicates possible suture zones where hybrid zones occur for many other organisms as well. These studies also provide clear genetic evidence of pre- and postglacial population expansions – particularly in North and Centre of the peninsula. Such advances from the coupling of modern phylogeography and paleogeology are very satisfying.

7.9 The Balkans: The Great European Hotspot

The Balkan Peninsula is less well-studied phylogeographically than Iberia or even Italy, but is richer in species and paleoendemics. This high taxonomic diversity was examined in a recent book, which is a first attempt to synthesize understanding of

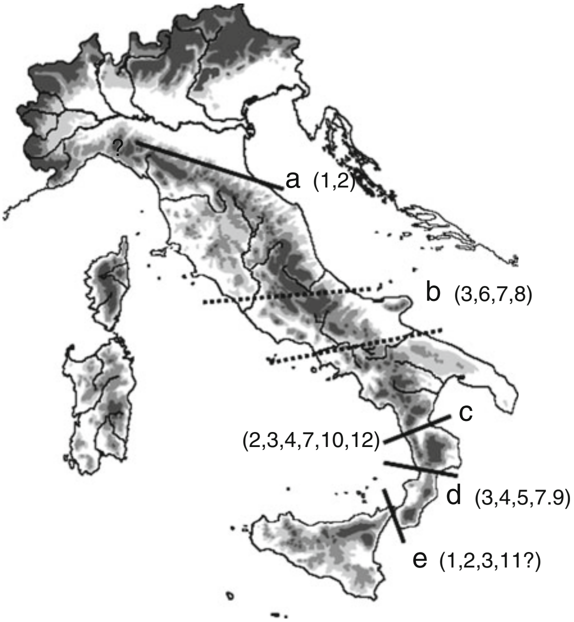

Fig. 7.3 *Geological and genetic dissection of the Italian Peninsula*. Species with distinct genetic types have been found subdivided at these places, indicating suture zones generated by Pleistocene range contractions and expansions, sea level changes and geological uplift. (**a**) The Po Valley; (**b**) South-Central region, between the Tiber and Volturno Rivers; (**c**) Crati-Sibiri Plain; (**d**) Catanzaro Plain; (**e**) Messina Straits. Species: 1, *Rana lessonae* – pond frog; 2, *Hyla intermedia* – tree frog; 3, *Rana italica* – stream frog; 4, *Bombina pachypus* – yellow-bellied toad; 5, *Hierophis viridiflavus* – whip snake; 6, *Zamenis lineatus* sp – Aesculapian snakes; 7, *Podarcis sicula* – wall lizard; 8, *Vipera aspis* – asp viper: 9, *Emys orbicularis* – pond turtle; 10, *Lacerta viridis* – green lizard; 11, *Chalcides chalcides* – three toed skink; 12, *Fagus sylvatica* – beech

biodiversity in this region (Griffiths et al. 2004). It has great importance for understanding and managing biodiversity since phylogeographic studies have shown that it was the major source of postglacial colonization of Central and Northern Europe. This makes the paucity of such information for the region itself both disappointing and frustrating.

The Balkan Peninsula and Hellenic region has a complex geological history, with its major orogeny occurring after the Pyrenees in the Eocene. Its subsequent development involved several land connections and submergences particularly through the Miocene and Pliocene (22–2 Mya), and the Aegean landmass comprising the Balkans (including Greece) and Turkey, was progressively broken up with the formation of the Aegean trench. The Paratethys Sea to the north was also dissected and reduced through this time. It is tempting to link such opportunities for dispersal and vicariance with the evolution of the region's high species diversity. There are a few recent phylogeographic investigations that address the evolution of species complexes in the region and demonstrate the progressive divergence of species, clades, and lineages through the Late Miocene, Pliocene, and Pleistocene – viz: *Triturus* (Babik et al. 2005), *Podarcis* (Poulakakis et al. 2005), *Mesotriton* (Sotiropoulos et al. 2007), *Rana* (Lymberakis et al. 2007), *Natrix* (Guicking et al. 2008), *Vipera* (Ursenbacher et al. (2008).

There are perhaps 15 clear cases for insects and vertebrates in the region where multiple Pleistocene refugia can be deduced from genetic data; *Chorthippus parallelus, Melanargia galathea, Parnassius mnemosyne, Drusus croaticus, Arion fuscus, Mesotriton alpinus, Testudo hermanni, Emys orbicularis, Bombina variegata, Lacerta viridis, Vipera ammodytes, Erinaceus concolor, Apodemus flavicollis, Dinaromys bogdanovi, and Lepus europaeus.* (Cooper et al. 1995; Schmitt et al. 2006; Gratton et al. 2008; Previsic et al. 2009; Pinceel et al. 2005; Sotiropoulos et al. 2007; Fritz et al. 2006; Joger et al. 2007; Hofman et al. 2007; Bohme et al. 2007; Ursenbacher et al. 2008; Seddon et al. 2001; Bugarski-Stanojevic et al. 2008; Krystufek et al. 2007; Fickel et al. 2008). No doubt many more will be reported with suitable phylogeographic investigation.

Two of these studies on Balkan endemics deserve note in that they show phylogeographic evidence of Late Pleistocene divergence and speciation within the Dinaric Alps – the endemic caddis flies *Drusus croaticus spp* (Previsic et al. 2009) and the paleoendemic Martino's Vole *Dinaromys bogdanovi* (Krystufek et al. 2007). Along with the older phylogenies they provide genetic evidence of the region's propensity for divergence and speciation, and emphasize its relevance today and for the future. Further detailed phylogeographic studies are sorely needed to clarify and establish such suggestions.

7.10 Age of Divergence and Speciation in the Peninsulas

There are endemic species in all peninsulas, particularly the Balkans and Iberia; this means that some organisms have been there for a long time and diverged to species and higher taxa. We have DNA divergence measures between species pairs in west and east Europe that allow broad estimates of the age of their initial divergence. Some are old divergences – e.g., *Natrix maura/tessellata* ~18 My, *Bombina bombina/variegata* ~5 My, *Erinaceus europaeus/concolor* ~6 My, and the others are younger examples from Pliocene and Pleistocene. There are several compilations from the general literature of genetic divergence in and between species (Hewitt 1996; Avise et al. 1998; Klicka and Zink 1999). The speciation rate in any individual case of course depends on the particular interplay of geography, selection, and chance that pertain, and may be very quick, but these estimates generally indicate some 2–3 My to form species. Thus there has been plenty of time in the formation of the Mediterranean region (~35 My) for much speciation in the Iberian and Balkan peninsulas and parts of the Italian peninsula.

Although there are many peninsular endemics that have diverged in the Miocene, Pliocene, and Pleistocene, it is interesting in contrast to consider those species widespread over much of Europe including all or most peninsulas. There are only some 20 for which there is sufficient phylogeographic data (see Table 7.1). The species complexes of *Natrix*, *Bombina, Triturus,* and *Erinaceus* are included since their taxonomic species contain clear phylogeographic information, and they exemplify the progression to distinct geographic species. All 20 of these show evidence of Balkan refugia, with 17 species colonizing central and northern Europe after the Last Ice Age. Some 14 colonized out of Iberian refugia into western and northern Europe, whereas only 6 colonized out of Italy. This emphasizes the major role of the Balkan and Iberian peninsulas in generating the biota of the northern half of Europe and the importance of the Alps as a barrier to postglacial spread. Some of the divergences are several million years old and before the Pleistocene, and all between taxa in species complexes. Most are in the Pleistocene, and many of these in the last few ice ages –for example, *Chorthippus*, *Ursus*, *Cervus*, *Lepus*, *Myotis*, *Strix*, *Capreolus*, *Apodemus,* and *Microtus*.

As well as fitting with the ~2 My for the divergence of taxonomic species, these data imply that quite a number of species have colonized some or all of the peninsulas recently. This in turn suggests the extinction of refugial populations in some recent ice ages, with recolonization from one surviving refugial source, or from outside Europe itself – probably from the East. This implies a greater flux of some species among peninsulas in the Late Pleistocene than had been imagined, possibly due to the increased ice age magnitude with 100 ky oscillation. Maybe such peninsular reseeding occurred for some species in earlier times, but the deep divergences in some and many endemics argue against it being universal or even common. It is the way of evolution that most lineages go extinct, and the many alleles of today are produced from fewer and fewer ancestors back through time. This means that we have much information on recent events and less on older ones.

7.11 Conclusions

The geological development of the Mediterranean peninsulas was complex and different, with Italy being young, the Balkans dissected, and Iberia old. The evolution of taxonomic diversity and phylogeographic structure of species in Europe reflects this in a number of ways – in lineage age, numbers of endemics, and refugial location through the Miocene, Pliocene, and Pleistocene. The complex mountain ranges of southern Europe are seen as particularly important in promoting divergence and speciation and retaining this diversity.

The peninsulas acted as refugia for many species through Pleistocene climatic oscillations, which were then able to colonize northern Europe during interglacials. The genetic signal of this recolonization is greatest from the Balkans and considerable from Iberia. The present biota north of the Mediterranean comprises elements from these southern refugia that are variously mixed in different regions.

The combination of detailed genetic and fossil data allows accurate location of particular refugia. For many species distinct genetic clades indicate multiple refugia in all three peninsulas, with particularly clear examples in West Iberia and Southern Italy. There has been occasional input of lineages and species from Africa and Asia to Europe, showing that species have colonized across the Straits of Gibraltar before, during, and after the Messinian Crisis. Divergent clades in several species in Southern Italy were probably produced by Late Pleistocene uplift and sea level changes. As the richest region for species and paleoendemics, more such work on the Balkan Peninsula is sorely needed.

Genetic divergence and speciation has occurred between and within peninsulas. The range of lineage ages indicates continuous divergence and speciation over many million years that has continued through recent ice ages. There are genetic examples of postglacial expansion in all peninsulas, and many species have shallow divergence among peninsulas suggesting recent recolonization. The peninsulas are important as long-term refugia for the survival of species and as engines of speciation. Future genetic investigations promise to greatly improve our understanding of these processes that produced these important hotspots.

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Chapter 8
Global Change Effects on Alpine Plant Diversity

Georg Grabherr, Michael Gottfried, and Harald Pauli

Abstract Alpine plants contribute considerably to the overall biodiversity. About 20% of the total European vascular plant flora is centred close to and/or above treelines. This high floral diversity for a cold environment depends predominantly on the pronounced heterogeneity of the terrain beyond the treeline. Alpine environments are also rich in endemics.

In this overview, we discuss the main drivers of biodiversity change (land use, climate change, and atmospheric composition).

Mountain dwellers have affected some mountain regions since prehistoric times, mainly in the old world (e.g. European mountains and Hindu Kush-Himalaya system) altering the mountain ecosystems, predominantly below treeline. In places such as the Alps, traditional land use systems enriched plant diversity locally. Land use change in regions such as the Alps or the Pyrenees leads to the loss of attractive elements of the cultural landscape such as pastures and hay meadows, because of abandonment or intensification.

Climate change in the future may affect many species including those living in unproductive and unused habitats. The observed warming of the past 150 years has already induced upward range extension of plant species, which, however, is not always in pace with the actual warming. Other impacts such as enhanced competition by invasive neophytes, eutrophication by airborne nitrogen, or higher atmospheric CO_2 might be relevant in the long term. So far, they are less effective than threats related to land use change.

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8.1 Introduction

8.1.1 *Mountains are Biodiversity Hot Spots*

As Barthlott et al. (1996) have highlighted, the mountains of the world are diversity hotspots for vascular plants. The main reason is the pronounced vertical climate zonation (Körner 2003; Nagy and Grabherr 2009). Under natural conditions, forests cover the valley bottom up to the treeline. The treeless alpine zone follows up to the limits of plant life. Scattered plant assemblages survive in the harsh environment of the so-called nival zone. Beyond the upper limit of higher plant life, only simple biota (bacteria, arthropods, and lichens) living of organic debris, blown in by the wind, exist. Plants confined to or centred in the alpine and nival zones contribute substantially to mountain biodiversity. Based on a sample of the Atlas Florae Europaeae (c. 10% of all Flora Europaea species), Väre et al. (2003) have estimated that ca. 2,500 vascular plant species, or 20% of the European total, were restricted to or centred in the area above the timberline; this area comprises about 3% of the continent. At the regional level similar figures are found. For example, the total flora of the Alps contains 3,983 native species (Aeschimann et al. 2004), of which 700–800 might be considered alpine in an ecological sense. The majority of endemics in the Alps are restricted to the alpine zone (270 of ~417 species; Ozenda and Borel 2003). The high-elevation vegetation of some Mediterranean mountains, such as the Sierra Nevada (Spain), is predominantly composed of endemic species (Pauli et al. 2003).

8.1.2 *Environmental Heterogeneity*

For a cold environment with average annual temperatures at or below +2°C, the overall richness is surprisingly high (Körner 2001). One reason is certainly the obvious high-environmental heterogeneity. A typical alpine zone landscape, e.g. that of the Alps (Fig. 8.1), consists of a matrix of dwarf shrubs and grasslands (Ellenberg 1996; Grabherr 1997; Jeník 1997; Nagy and Grabherr 2009). Interspersed are corridor-like structures such as rivers, ridges, and patch-like elements such as snow beds, fens and mires, and little lakes. Rock outcrops, rock faces, screes, and talus slopes complement the habitat mosaic. Vegetation varies in relation to exposure, and soil conditions. The content of carbonates is one of the most differentiating factors (Gigon 1971) for species composition and diversity. From the Austrian Alps, 42 alpine grassland community types (associations), eight dwarf shrub heath, and eight snow bed communities, >60 communities on screes or rock faces, and 11 tall forb communities from nutrient-enriched soils (e.g. resting areas of animals and avalanche pathways) have been described (Grabherr and Mucina 1993).

Fig. 8.1 Habitat heterogeneity in a typical alpine (above treeline) landscape in the Alps: dominating grasslands (different colours show diverse communities), rock faces, screes, rocky and wind swept ridges, snow beds, fens and mires, and lakes. Note also the difference of the rock colours indicating siliceous bedrock material in the foreground and calcareous in the background. The highest summit on the right side extends into the nival zone

8.1.3 Mountain Environments: A Global Perspective

In a global perspective, mountains show a great variability in the combination of elevation (air density), climate seasonality, and water availability (Nagy and Grabherr 2009). Different dominant growth forms are the conspicuous expression: giant rosette plants in the perhumid tropics (páramo), tall tussock grasslands in the tropical (puna) and temperate southern hemisphere, shrubby cushion heath in the subtropics, and alpine tundra (dwarf shrub heath, grasslands with sedges, rushes, but less grasses) in the temperate to arctic northern hemisphere. The vascular plant species richness of these vegetation types varies considerably from <10 up to 50 species per vegetation plot (the plot size varied from 10 to >100 m according to the "minimum area" that includes 90% of species of the particular plant community). Within-community species richness of middle latitude alpine grasslands can be considerably higher than that of tropical alpine páramos and tussock grasslands (Grabherr et al. 1995).

8.1.4 The Human Influence

In Europe, it is a commonly held paradigm that land use has increased biodiversity in mountain regions (e.g. Bätzing 2003), especially as agrobiodiversity has become a focus of interest, and an argument for environmental subsidies (Bardsley and

Thomas 2004). It depends, however, on the scale one considers biodiversity. For example, for the Alps as a whole and the alpine pastureland in particular, the old settlers with their livestock have, with the exceptions of introducing some weeds, not really altered the native plant stock significantly (Erschbamer et al. 2003). All pasture species can be found in natural non-pastured habitats as well. On the local scale, however, they created new biotic communities forming a cultural landscape of fields, meadows, pastures, and remaining forests (Bätzing 2003; Wrbka et al. 2004). The diversity of land use types is positively correlated with species richness (Stöcklin et al. 2007). For the Alps and other mountains of Europe (Carpathians, Pyrenees, and Caucasus), the most valuable product of human activity from a biodiversity point of view has been mountain hay meadows, cut on average once a year. These meadows are rich in species, many of which are very showy (Fig. 8.2). Such beautiful meadows certainly owe to some extent their existence to human interference, and therefore, their continued dynamics are dependent on management. The species forming the meadow, however, originate from natural sources such as avalanche meadows, rock outcrops, alpine grassland, and heath.

Man-made hay meadows of this type are more or less restricted to the humid-temperate mountains of Europe. In other regions (see Spehn et al. 2006; Nagy and Grabherr 2009 for an overview and case studies), transhumance systems use high summer pastures, and snow-free pastures in the lowlands during winter (mountains of Central Asia and Hindu Kush-Himalaya system). Such transhumance systems were formerly also existing in some parts of Europe. In the mountains of High Asia, collecting medicinal plants complements pasturing, and, as it has recently become a

Fig. 8.2 Typical species-rich mountain hay meadow at Tannberg, Austrian Alps. These meadows are mown once or twice a year, sometimes less. Hay was stored in shelters and brought down to the valleys in winter time – a very dangerous job. Many of these attractive and species-rich meadows (>50 species per 25 m^2) have been left abandoned or are now fertilised and mown more frequently. Maintaining the meadow culture is certainly one of the main challenges for nature conservation in the Alps (Photo: Markus Grabher, UMG – Umweltbüro Grabher)

"cash crop"-type commodity, it may lead to excessive harvesting and endangering rare species such as snow lotus (*Saussurea*). Tibetan doctors use 67% of alpine plant species (Salick et al. 2009), many more than used by natural healers in the Alps (Grabherr 2009). The puna and páramo ecosystems of the Andean highlands have been affected by the introduction of new animals (ovines and bovines) after the Spanish conquest (Molinillo and Monasterio 2006). The former camelid grazer systems were adapted to the natural vegetation. Overgrazing by the unadapted new animals resulted in severe damage. In other parts of the world, extensive mountain regions have remained where the alpine and nival environments are still in a pristine state (Rocky Mountains, Patagonian Andes, and Japanese and New Zealand Alps).

8.1.5 Drivers of Change

A global modelling study (Sala et al. (2000) evaluated the importance of land use change, climate change, N-deposition, biotic exchange, and increasing atmospheric CO_2 regarding the sensitivity of biodiversity to these changes. They concluded that globally, land use change impacts will probably have the largest effect. The particular life zones, however, may differ from each other. According to Sala et al. (2000), arctic and alpine environments and biota will be affected most by climate change. This, however, is not generally valid. Grötzbach and Stadel (1997) classified the recent state of the world's mountains from a human geographical point of view as follows: (1) recently and sparsely settled mountains, for which the categorisation of Sala et al. (2000) holds true, (2) prehistorically settled mountains with still intact subsistence agriculture and a tendency to overpopulation, (3) highly developed regions such as the Alps, and (4) mountains in transition in the former collectivised systems in communist countries of Eurasia. Significant changes driven by land use are ongoing in the third and fourth type, climate and land use driven changes are expected in the second, and climate driven in the first type. Here, we discuss the effects of land use change in the Alps, especially that of the introduction of modern mountain farming. Effects of climate change in a global context will be explored and evidence for already observable impacts is presented. Finally, some short comments on biotic exchange, N-deposition, and CO_2 enrichment are made.

8.2 Effects of Land Use Change on Biodiversity: The Alps

With the exception of transhumance in the south-western Alps, traditional subsistent farming systems in the Alps depended on storage of food for people and fodder for the livestock to survive long and snowy winters. Forests on the slopes were cleared and transferred into hay meadows and arable land; cereals were grown nearly up to the treeline. Summer pasturing close to the treeline on former forests and beyond the treeline up to the glaciers was, and partly is still common practice, being an essential complement to the limited resources in the valleys. Steep grassy slopes in the subalpine and alpine zones were mown in late summer, contributing to the winter storage. In all six of the farming types distinguished by Bätzing (2003), the transfer of biomass between the high grounds and the valleys is the common character of mountain farming in the Alps and in temperate mountains in general.

The traditional mountain world has changed (Bätzing 2003), and no village in the Alps has been left whose economy depends exclusively on agriculture. In the east, south, and south–west, the populations have decreased during the past century. Below the treeline, much land has become abandoned and is in the process of reverting to forest. Above the treeline, alpine heath and grassland do not change in species composition substantially after abandonment. They may, however, lose some of their attractiveness to the observer. As with hay meadows, species richness in the Hohe Tauern, Austria (1,800–2,200 m) lost about 30% of the originally 55 species after abandonment, and attractiveness, measured as number of inflorescences per m^2 (100% = 50), was reduced by more than 50% (Abl 2003). In the long term, both species richness and inflorescence frequency increase again as new species invade. None of the meadow species is critically endangered at the regional level as populations in natural habitats such as steep, rocky slopes, and avalanche tracks occur. However, a unique, species-rich, and beautiful cultural plant assemblage disappears. Besides its beauty and diversity, it is the cultural value of these meadows and landscapes as a whole which needs conservation action. Transforming them into wilderness is another option as discussed in detail for the Val Grande National Park in Italy by Höchtl et al. (2005). The authors conclude that wilderness is a too vague concept, and should be replaced by exploring the different options in relation to improve naturalness or a kind of cultural heritage.

Another reason for maintaining such meadows and alpine pastures might be that less species means reduced slope stability (Körner 2002). Tasser et al. (2003) found a decrease in root density, change in cover of grasses, and dwarf shrubs on abandoned slopes, and concluded that suchlike transformed vegetation resisted less well erosive activities. This might hold true for the particular research location, but should be tested at a much broader scale, considering the enormous heterogeneity of the alpine terrain. Some erosion patches may "heal" quite rapidly as grasses such as *Agrostis schraderiana* invade by tillering (Grabherr et al. 1988).

Globally, however, overgrazing has appeared to be a true problem in regions with increasing populations (Central Asia, Himalayas, seasonal-tropical Andes; Spehn et al. 2006).

Much support has been given to mountain farmers in recent years to maintain farming in the Alps (Bardsley and Thomas 2004). Meadows, as described, are so-called habitats of community interest in the European Union. Today, dairy farming remains the basic type of farming (e.g. most of Switzerland, western Austria, Bavaria, and South Tyrol), and many farmers tend to increase productivity by modern dairy breeds. In Vorarlberg (Austria), one of the lead regions in dairy

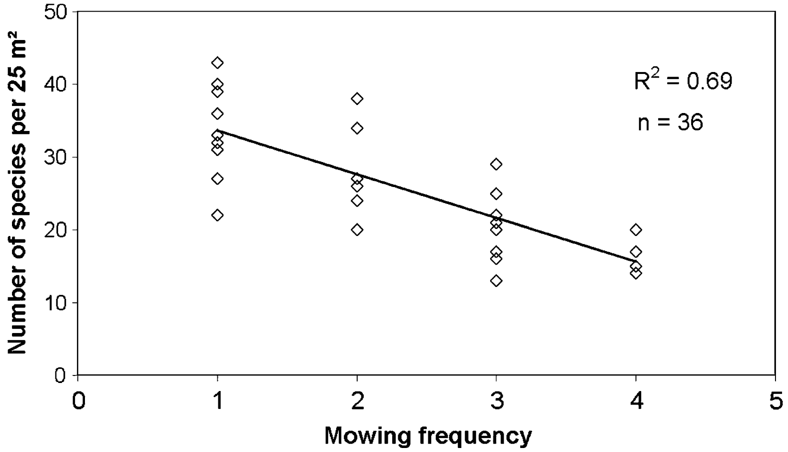

Fig. 8.3 Species richness of mountain meadows depends on mowing frequency as exemplified here from mountain farms in Vorarlberg. Austria (UMG – Umweltbüro Grabher 2004, unpublished data)

farming, the average production of milk per dairy cattle has increased from about 4,500 l per annum in 1990 to about 7,000 l today. Such high performance breeds require energy-rich fodder (silage, cereals, corn, and soybean extract). Hay meadows are fertilised and mown several times a year to produce silage, and this decreases species richness (Fig. 8.3, Stöcklin et al. 2007, p. 72) and attractiveness. As a consequence, much of the alpine species-rich meadows and pastures are nowadays replaced by monotonous green, species-poor grasslands. At one of the most famous high-elevation mountain farmland, the Seiser Alm in South Tyrol, Italy (1,800–2,300 m, 5,150 ha), fertilising with manure and/or mineral fertiliser has reduced species richness by more than 50% per plot since the 1950s (Grabherr et al. 1988). The average richness of the traditional meadows was found to be 50 ± 9 species per 20 m^2, and that of fertilised ones to be 22 ± 5 species per 20 m^2, where the latter were mostly composed of grasses or weedy species (Table 8.1). At Seiser Alm, a loss of >50 million individuals of showy attractive alpine plant flowers in fertilised meadows during the last 40 years were estimated, including the disappearance of at least six million individuals of blue gentians – *Gentiana acaulis* (Grabherr 1993).

Mountain agriculture, where it is practised, is certainly the most important factor in determining montane to subalpine plant diversity over large areas. Much more so than tourism, which is relevant only locally in damaging populations of rare species or deteriorating alpine landscapes by trampled tracks, ski runs, access roads, or buildings. Conservation measures were obviously effective in some cases; e.g. plant species such as Edelweiß (*Leontopodium alpinum*) that before conservation legislation were critically endangered in some regions by excessive collecting are found in healthy populations nowadays (G. Grabherr, personal observation).

Table 8.1 Vegetation table of 123 vegetation samples (20 m^2 each) from Seiseralm, South Tyrol, Italy (modified after Grabherr et al. 1985). Species: (1) characteristic grasses (*italics*), (2) attractive species (*bold*). *Roman figures* are constancy values (I 1–20%, II 20–40%, III 40–60%, IV 60–80%, and V 80–100% constancy). The table shows that fertilising considerably reduces species richness and attractiveness of mountain meadows

	Nutrient-poor pasture	Nutrient-poor meadow	Moderately poor meadow	Fertilised meadow
Avenochloa vesicolor	**IV**	I	I	–
Avenella flexuosa	**V**	II	II	I
Geum montanum	**V**	I	–	–
Trifolium alpinum	**IV**	II	I	–
Phytheuma hemispaericum	**III**	**–**	–	–
Hypochoeris uniflora	**II**	**–**	I	–
Veronica bellidioides	**II**	**–**	–	–
Nardus stricta	**V**	**V**	III	–
Pulsatilla vernalis	**IV**	**III**	I	–
Calluna vulgaris	**III**	**III**	I	–
Antennaria dioica	**IV**	**III**	II	–
Avenochloa pratensis	I	**IV**	**III**	I
Carex sempervirens	II	**III**	**IV**	I
Briza media	II	**IV**	**IV**	II
Trifolium montanum	I	**V**	**IV**	I
Knautia longifolia	II	**IV**	**IV**	II
Hieracium pilosella	III	**IV**	**III**	–
Plantago media	I	**V**	**IV**	I
Pimpinella saxifraga	–	**III**	**II**	–
Hippocrepis comosa	–	**III**	**II**	–
Rhinanthus aristatus	I	**III**	**III**	I
Daphne striata	I	**V**	I	–
Thymus praecox	II	**V**	II	–
Prunella vulgaris	I	**V**	II	–
Potentilla crantzii	I	**IV**	I	–
Carduus defloratus	I	**IV**	II	–
Polygala chamaebuxus	I	**III**	I	–
Trifolium badium	I	–	**V**	II
Sanguisorba officinalis	I	–	**IV**	III
Pedicularis verticillata	II	–	**III**	I
Horminum pyrenaicum	–	–	**II**	–
Festuca halleri	III	II	IV	II
Arnica montana	**V**	**III**	**IV**	–
Campanula barbata	**IV**	**III**	**IV**	–
Gentiana acaulis	**IV**	**V**	**IV**	–
Carlina acaulis	**IV**	**V**	**IV**	–
Anthyllis vulneraria	**III**	**V**	**IV**	–
Pulsatilla apiifolia	**IV**	**I**	**III**	I
Poa alpina	**II**	**I**	**IV**	**V**
Crepis aurea	**III**	**–**	**IV**	**V**
Trollius europaeus	**II**	**I**	**V**	**IV**

(continued)

Table 8.1 (continued)

	Nutrient-poor pasture	Nutrient-poor meadow	Moderately poor meadow	Fertilised meadow
Myosotis alpestris	**III**	**I**	**IV**	**III**
Poa pratensis	–	–	I	**III**
Poa annua	–	–	I	**III**
Festuca nigrescens	**IV**	**V**	**V**	**IV**
Trifolium pratense	**V**	**V**	**V**	**IV**
Leucanthemum vulgare	**IV**	**III**	**V**	**III**
Leontodon hispidus	**IV**	**IV**	**V**	**III**

8.3 Impacts of Climate Change: The New Threat

Many alpine plant species that occur in Red Lists are classified as potentially endangered. A large number of them are endemics, many of them growing in habitats which have little real or potential economic interest. Nonetheless, and particularly if they are restricted to few sites, they have to be considered as potentially sensitive to climate change.

Much evidence has accumulated that alpine biota have been responding to the warming since the end of the Little Ice Age around 1850. Enhanced tree growth at treeline ecotones in the Urals (Moiseev and Shiyatov 2003), the Scandes (Kullman 2001, 2002, 2008), and in the Rocky Mountains (Klasner and Fagre 2002) has lead to a filling and slight upward moving of the treeline ecotone.

At the limits of vascular plant growth, i.e. at high summits of the Alps and Scandes species richness has increased (Grabherr et al. 1994; Bahn and Körner 2003; Klanderud and Birks 2003; Pauli et al. 2007; Holzinger et al. 2008; Erschbamer et al. 2009; Vittoz et al. 2008), indicating the expected upward range expansion induced by warming. That warming is at least one of the causes is supported by the fact that the exceptional warm years of the past two decades have accelerated this process (Walther et al. 2005). The rate of upward shifts, however, does not keep pace with potential moving rates projected from the actual increase in temperature (Grabherr et al. 1994).

There are complex causal factors behind vegetation change. At treeline, warmer temperatures may increase growth of young trees directly as photosynthetic gain increases (Butler et al. 2009; Malanson et al. 2007), but will also favour root respiration in the now warmer soils (Körner and Hoch 2006), which affects the growth. Most important in alpine environments, however, is that much of the precipitation falls as snow. Particularly, the limits of plant life are determined by long snow line, which reduces reproductive success. On the other hand, snow protects the plants from severe winter frosts and during cold spells in the growing season, when temperature may drop below lethal values (Larcher et al. 2010). Less precipitation in combination with warming is predicted to have the highest impact on the high alpine–nival flora (Gottfried et al. 2002).

Model scenarios predict that a warming-induced upward migration may push some species to the point of “nowhere to go” (Loarie et al. 2009). Continent-wide projections using large grid cells have estimated an extinction rate of more than 60% for some European mountain regions (Thuiller et al. 2005). In the New Zealand Alps, a warming of about 3°C might cause a loss of 200–300 indigenous alpine species (Halloy and Mark 2003). In some micro-refugia, however, some species may survive as projected by Gottfried et al. (1999) for alpine/nival species at the GLORIA master site Schrankogel. Randin et al. (2009) have undertaken a modelling experiment at different scales, where the fine-scaled model suggested that some suitable habitats would remain for all alpine species at least in the particularly high Alps of Valais (Switzerland). Further, alpine and subalpine biota, such as *Pinus mugo* communities in the Eastern Alps, may be very persistent and could considerably delay invasion of new competitors from lower elevation (Dullinger et al. 2004).

Low impact on subalpine grassland in Switzerland suggests that late successional communities are quite stable (Vittoz et al. 2009). Britton et al. (2009), however, found an increase in species richness in Scottish alpine vegetation, but a concurrent decline in beta-diversity over the past 20–40 years, resulting in an increased homogeneity of vegetation. Changes of alpine to nival summit floras in the Alps may also indicate a trend towards homogenization (Jurasinski and Kreyling 2007). Moreover, a clear decrease in cover of the cryoflora at the limit of plant growth at Mt. Schrankogel (Tyrol) was found between 1994 and 2004, mainly in open plant assemblages, where effects of competition are of inferior relevance (Pauli et al. 2007). Some alpine grassland pioneers have increased in cover, whereas all true nival species have declined at the alpine–nival ecotone of Mt. Schrankogel.

Diverging and contradictory model predictions and results of observation studies are not surprising, given the complexity of alpine diversity patterns and due to the scarce data sources. Systematic, coordinated, and long-term monitoring approaches, however, have only recently been implemented, e.g. GLORIA (http://www.gloria.ac.at/) and MIREN (http://www.miren.ethz.ch/). So far, probably, not one alpine species has become extinct through recent climate warming; however, in the longer term many alpines may be at risk to suffer habitat losses (Theurillat and Guison 2001), particularly where the alpine zone is limited. Examples are the Australian Snowy mountains whose alpine zone is restricted to 370 km^2 (Johnston and Pickering 2001), and the Sierra Nevada in Spain (Pauli et al. 2003). In both cases, the total loss of a unique alpine flora seems not to be unrealistic.

8.4 Biotic Exchange (Neobiota), N-Deposition, and CO$_2$-Enrichment

Alpine biota are among the least affected by invasive alien species. In a comprehensive comparison of habitats from Europe, Chytry et al. (2008) found not one neophyte in the alpine grassland dataset. The absence of neobiota in alpine environments may hold true in habitats such as dwarf shrub heath, rocks, and screes (e.g. Walther et al. 2005; Rabitsch and Essl 2006 for Austria; Vila et al. 2007 for Catalonia). The harsh alpine conditions do not favour fast growing ruderals or competitors, which prefer disturbed, nutrient rich, and warm habitats. Becker et al. (2005) discussed the decline of neophytes with increasing elevation in Switzerland in relation to theoretical concepts, i.e. the low-altitude filter effects, low propagule pressure, and genetic swamping in peripheral populations, but did not derive any definitive conclusions on the relative importance of these effects. In Australia, however, the very small alpine zone is a place where neophytes might become a risk to the native flora. So far, 175 neophytes have been recorded beyond 1,500 m a.s.l., with ten species in the alpine zone (Johnston and Pickering 2001). How these alien species will become a severe threat to the natives, however, remains a "guesswork" as the authors state (see also McDougall et al. 2005).

Airborne nitrogen will affect alpine plant communities, as can be deduced from experimental nitrogen addition experiments (e.g. Nagy and Proctor 1997; Bowman and Seastedt 2001; Körner 2001; Heer and Körner 2002). An addition of 40 kg N per ha during the growing season increased growth of sensitive species, which might overgrow small-stature species (Körner 2000). This amount, however, is far above that to be expected in the almost remote mountain regions (Bowman and Seastedt 2001). Observations and experiments at the alpine research site Niwot Ridge showed evidence that not only vascular plants are affected, but also the species composition of microbial communities which moderate N-cycling.

As available CO_2 is reduced at high elevations (low partial pressure), enhanced CO_2 content should favour growth of alpine/nival plant species. In situ experiments, however, suggest that this is not the case in the long term. Above-ground biomass at a typical grassland site in the Swiss Alps did not increase under double CO_2 and below-ground biomass to a low extent (Körner et al. 1997). Grace et al. (2002) stated that enhanced CO_2 increased nitrogen deposition, and temperature co-varies, and their effects cannot be disentangled. Feedbacks and cascade processes determine reactions at the ecosystem level (Wookey et al. 2008).

8.5 Outlook

Alpine environments are among the few which are still in a near-natural state, and not substantially altered. High mountain farming in the traditional form has had some influence, creating diverse and attractive plant communities such as the hay meadows in temperate mountain regions or the extensive pastures, if not overexploited, in nearly all permanently settled mountain regions. What matters from the biodiversity conservation point of view is to maintain the traditional richness of dependent habitats by supporting sustainable agriculture. Specific support regimes have to be applied to reach this challenge.

Whenever most alpine plant species, including most endemics, have been on the safe side so far, this will change in a changing climate. Predicted large-scale mass extinction, however, may not be a realistic scenario as there are many ways species may cope with warmer climates, such as survival in micro-refugia, resistance against competition, e.g. via their morphology (clonal systems). Some species, however, certainly face a risky future. Where mountains are in close vicinity to industrial centres, the input of nitrogen will enhance the warming effect. Mediated by an accelerating warming, neophytes will have an increasing chance to expand to formerly alpine environments.

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Chapter 9
European Hotspots as Evidenced by the Palearctic Distribution of Songbirds

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Abstract A database has been created of digitized equal area distribution maps of 2,401 phylogenetic species of songbirds endemic to the Palearctic Region. Geographic distribution of species richness delineated several hotspot regions in the Palearctic, mostly located in mountainous areas. The index of range-size rarity generally identified similar hotspot regions as that for species richness, although it de-emphasized the large central-Siberian hotspot. The hypothesis was tested that databases restricted to a non-natural biogeographic region, such as "Europe," will identify a different set of hotspots, as compared with a spatial analysis of a more natural biogeographic region such as the Palearctic. For that purpose, only those taxa from the dataset were selected that occur in the geographic region delimited by the EBCC atlas and the Climatic Atlas of European Breeding Birds, in total 516 taxa. European hotspots of species richness were slightly more prominent in the Palearctic dataset as compared with the European dataset of 516 taxa. The index of range-size rarity indicated a more pronounced difference between the hotspots identified by the Palearctic dataset and the European dataset, with little or no differentiation in the latter. It is concluded that the present qualitative analysis suggests that it is important for hotspot and conservation studies to examine a natural biogeographic region, and not a geopolitical entity such as "Europe."

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9.1 Introduction

We have compiled a database of digitized distribution maps of breeding areas of songbirds of the Palearctic Region with the help of the biogeographic program WORLDMAP (Williams 2000a). The geographic distributions were interactively plotted on an equal area map of the Palearctic; each grid cell covers 16,246 km^2 (cf. Roselaar et al. 2007). Our base map covers an area that is somewhat larger than the traditional demarcation of the Palearctic Region, but recently Roselaar (2006) argued that the southern boundary of the Palearctic should be drawn along the lowermost boundary of our map, at least on the African continent. Furthermore, birds in Greenland, the Philippines, and Alaska were not mapped, because these areas do not belong to the Palearctic Region.

For our descriptor of species level diversity, we have chosen the phylogenetic species concept. Our full database contains maps for 3,036 of such phylogenetic species; these maps are based on information from museum specimens and also on a large amount of data from the literature.

Evidently, our database contains many Oriental and Afrotropical species that have their main distribution outside of the Palearctic Region, what we call “partly extra-limital” ranges or species. When we delete these partly extra-limital species from our database, a set of 2,401 taxa remains that is really endemic to the Palearctic Region.

A second dataset was made by selecting those species that occur as breeding birds in the geographic region covered by the EBBC atlas (Hagemeyer and Blair 1997) and, subsequently, also by the Climatic Atlas of European Birds (Huntley et al. 2007). This dataset contains 516 species. There is, however, one difference between our second, Europe-focussed dataset and the EBBC data. For example, EBBC does not consider Turkey at all. When in our dataset, however, a bird occurs outside of Turkey but also within Turkey, we left all records in the database. This means that in our dataset the European taxa are represented with their entire Palearctic distribution.

With the help of these datasets, we will determine hotspots of species richness and hotspots of endemism or range-size rarity. Hotspots of species richness are chosen by counting the numbers of species in each grid cell, subsequently ranking the cells by this count, and selecting the higher scoring cells. Hotspots of range-size rarity are determined by calculating the sum of the inverse of the range sizes. A species recorded from 1 cell has the maximum score of 1, a species occurring in 10 cells scores 0.1, from 100 cells 0.01, etc. For each grid cell, the weights are added up for all species occurring in this cell. Effectively, this measure of range-size rarity gives greater weight to the most restricted species, with the widespread species having little effect on the scores (Williams 2000b).

9.2 Hypothesis Testing

Specifically, for the present study, we aim to qualitatively test the following hypothesis. It is evident that the geographic region covered by the EBBC atlas is a biologically and biogeographically artificial part of the Palearctic Region. Basically, it is a geopolitical part of Europe and not a natural biogeographic entity that relates to the natural distribution of the species. It is our hypothesis that such an unnatural selection of a set of species must result in a biased determination of European hotspots. We postulate that consideration of all songbirds across the entire Palearctic Region will produce a more realistic, natural, and balanced delineation of biodiversity hotspots, also within Europe.

9.3 Palearctic Hotspots

Before zooming in on Europe, first, we wish to document the Palearctic hotspots as evidenced by our database. The scores for the index of species richness for our subset of 2,401 taxa endemic to the Palearctic region are visualized in Fig. 9.1. Red represents the highest score and dark blue the lowest. In the present context, we refrain from discussing this result in detail, but only point out the large hotspot in central Siberia and hotspot areas along the Himalayas. Closer to Europe, there is a hotspot area south of the Caspian Sea.

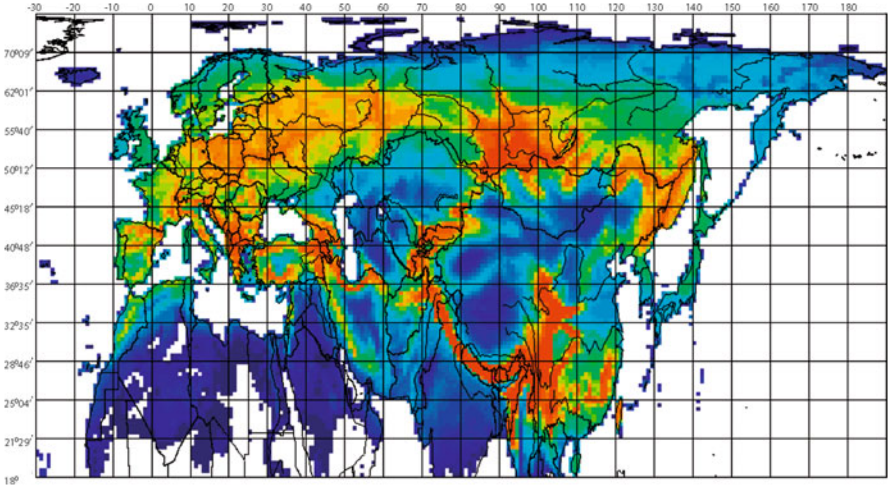

Fig. 9.1 Map of species richness among equal area grid cells in 2,401 phylogenetic species of Palearctic songbirds. Maximum richness shown in *deep rufous* and minimum in *dark blue*. Scores grouped into 32 color-scale classes of approximately equal frequency

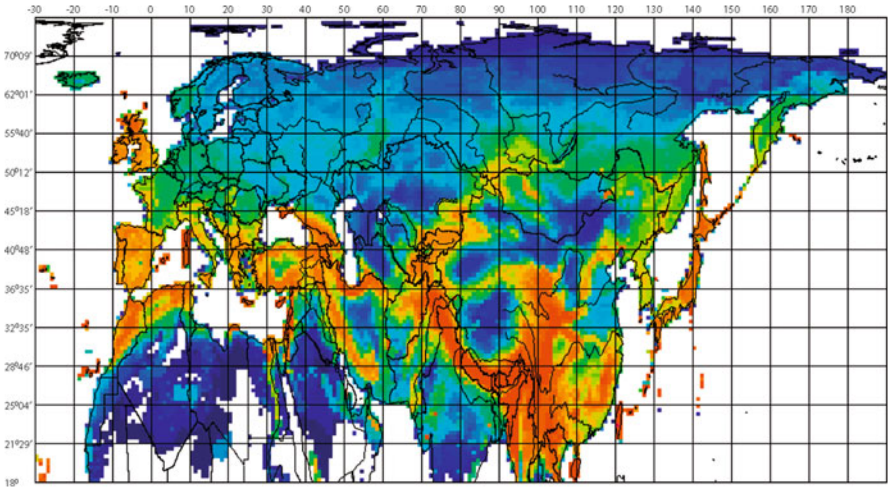

Fig. 9.2 Map of geographic variation in range-size rarity scores among equal area grid cells in 2,401 phylogenetic species of Palearctic songbirds. Scores are grouped into 32 color-scale classes, each of which contains approximately equal numbers of grid cells on a gliding scale ranging from 0.00% to 4.34%, with a separate single grid cell for the maximum score (4.35%)

When we consider another measure or index of biodiversity, endemism or range-size rarity, the pattern depicted in Fig. 9.2 emerges. A notable difference with Fig. 9.1 is that the central-Siberian hotspot has disappeared. For the rest, the results for endemism are rather similar to the hotspots of species richness, with the difference that on the index of range-size rarity many islands are much more prominent as hotspots. That effect is even clear for the British Isles. Another clear difference with species richness is that the Atlas Mountains in North Africa score high on range-size rarity.

9.4 Europe

First, we will compare the European hotspots as identified with the Palearctic dataset of 2,401 taxa with the European hotspots identified with the restricted dataset of the 516 taxa in our database that occur in the region covered by the EBBC atlas. The first dataset we will call the Palearctic dataset and the 516 taxa will be referred to as the European dataset.

The results for species richness are presented in Fig. 9.3a, b. It appears that there is a difference between the two datasets, but it is only in that the hotspots for the European dataset are less pronounced than those determined with the Palearctic dataset. We see that, for example, in both cases, sections of the Balkan score high, and also the Caucasus.

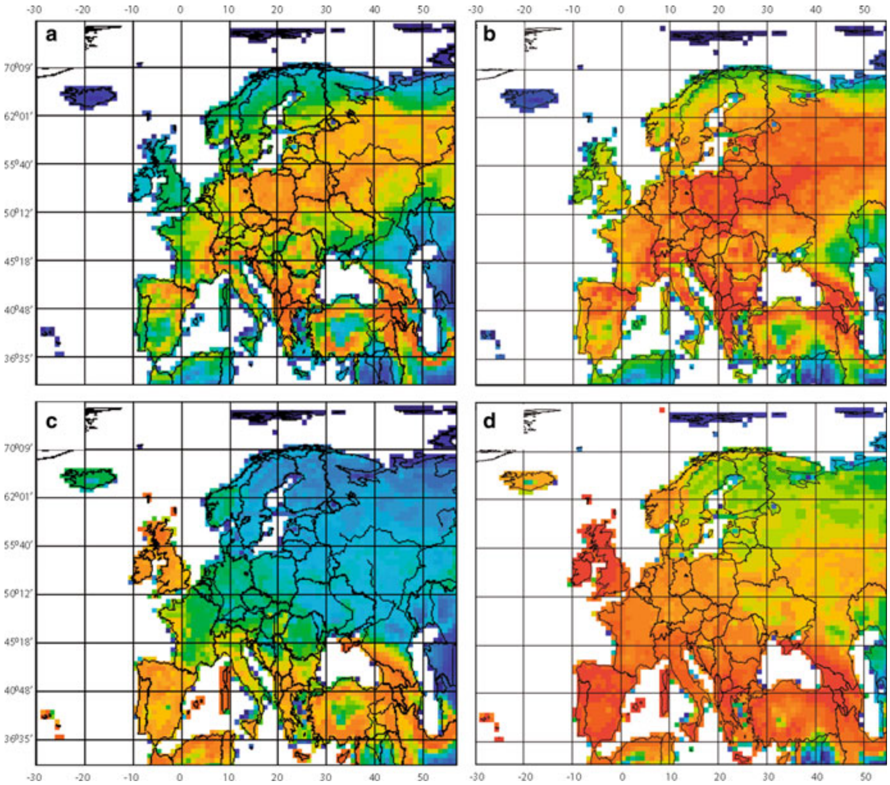

Fig. 9.3 (**a**) Map of species richness among equal area grid cells in 2,401 phylogenetic species of Palearctic songbirds; see Fig. 9.1. (**b**) Map of Species Richness among equal area grid cells in 516 phylogenetic species of European songbirds. Maximum richness is shown in *deep rufous* and minimum in *dark blue*. Scores grouped into 32 color-scale classes of approximately equal frequency. (**c**) Map of geographic variation in range-size rarity scores among equal area grid cells in 2,401 phylogenetic species of Palearctic songbirds; see Fig. 9.2. (**d**) Map of geographic variation in range-size rarity scores among equal area grid cells in 516 phylogenetic species of European songbirds. Scores are grouped into 33 color-scale classes, each of which contains approximately equal numbers of grid cells on a gliding scale ranging from 0.00% to 15.50%; highest scores in *red*, lowest in *dark blue*

When we look at the important index of biodiversity that relates to local endemism, or range-size rarity, the picture becomes different (Fig. 9.3c, d). We see that the Palearctic dataset identifies several regions of Europe as important hotspots, such as the British Isles, the Iberian Peninsula, Corsica, and Sardinia. However, that effect is hardly deduceable from the European dataset. The effect is somewhat clearer when we restrict our analysis to the 25% of the species with the smallest ranges, the first-range quartile. In the Palearctic dataset, Corsica and Sardinia are very prominent hotspots (Fig. 9.4a), and this is also the case with the European dataset (Fig. 9.4b). But there are also differences. In the European dataset, for example, the British Isles suddenly score very high on the first-range quartile.

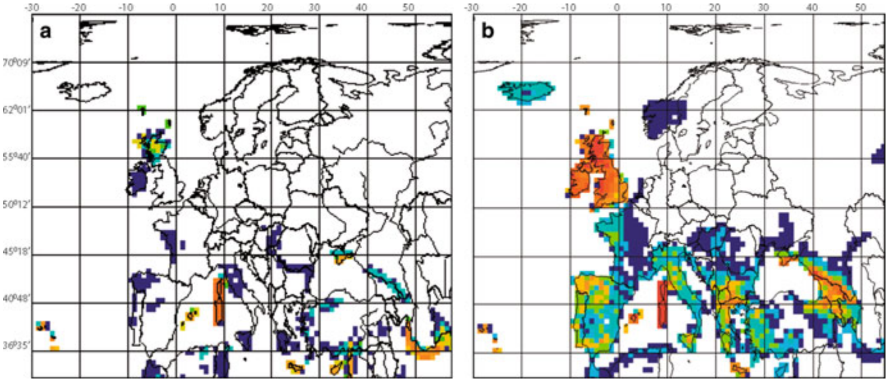

Fig. 9.4 Maps of geographic variation in range-size rarity scores among equal area grid cells for the Rare Quartile of species with most restricted distributions, determined by numbers of occupied grid cells; partly extra-limital species are excluded. Scores are grouped into ten color-scale classes, each occurring in about equal frequency; highest scores in red, lowest in dark blue. (**a**) Palearctic dataset. (**b**) European dataset

9.5 Comparisons

It will be interesting to compare our results with other analyses that focussed on Europe, or on the Palearctic Region, or even on a global level. There are a few comparsions that we can make between the hotspots identified with our Palearctic and European datasets on the one hand and global hotspot studies on the other hand. For example, hotspot studies have been done by Conservation International (cf. Mittermeier et al. 1999, 2004). In the present context, we will focus only on the European part of their worldwide analysis. First of all, in 2004, these workers did considerably broaden their hotspot regions in comparison with their 1999 study (Figs. 9.5a, b). When we compare this with our results for species richness and range-size rarity for the Palearctic dataset (Fig. 9.3a,c), it is evident that particularly the index on range-size rarity selects many hotspot regions that are also present in the 2004 analysis of Conservation International, notably Spain, Corsica and Sardinia, Turkey, and the Caucasus. In contrast, the species richness result for our European dataset (Fig. 9.3b) shows much less conformity with the hotspots of Conservation International, because there are major parts of central Europe that score rather high, in contrast with the analysis of Conservation International.

From an ornithological perspective, it is interesting to compare our results with the Endemic Bird Areas as determined by BirdLife International (cf. Stattersfield et al. 1998; Fig. 9.6). There are only two European areas that qualified as Endemic Bird Area in the study of BirdLife International, viz. Cyprus and the Caucasus. But Cyprus is not covered by the EBBC atlas! Furthermore, in our European dataset of 516 taxa (more or less comparable to the EBBC selection), Cyprus turns out to be a coldspot on the index of species richness, while that of range-size rarity does not

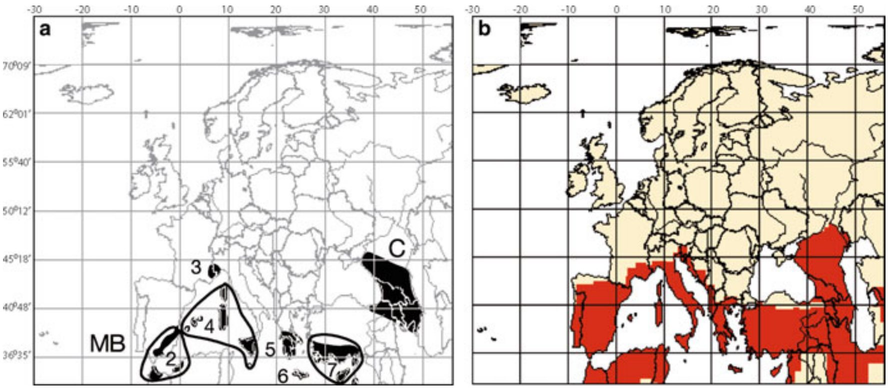

Fig. 9.5 (**a**) Hotspot areas as identified and codified by Mittermeier et al. (1999) for Europe, the Middle East, and North Africa and projected on our map: MB (Mediterranean Basin): (2) Rif Bétique and coastal strips in Morocco and Algeria, (3) Maritime Alps, (4) Tyrrhenian Islands, (5) south and central Greece, (6) Crete, and (7) southern Turkey and Cyprus (Note: the numbering follows the table on p. 256 in Mittermeier et al. and not the incorrect numbering and legend on p. 255); C (Caucasus). (**b**) Hotspot areas as identified by Mittermeier et al. (2004) for Europe, the Middle East, and North Africa, projected on our map of the Palearctic Region

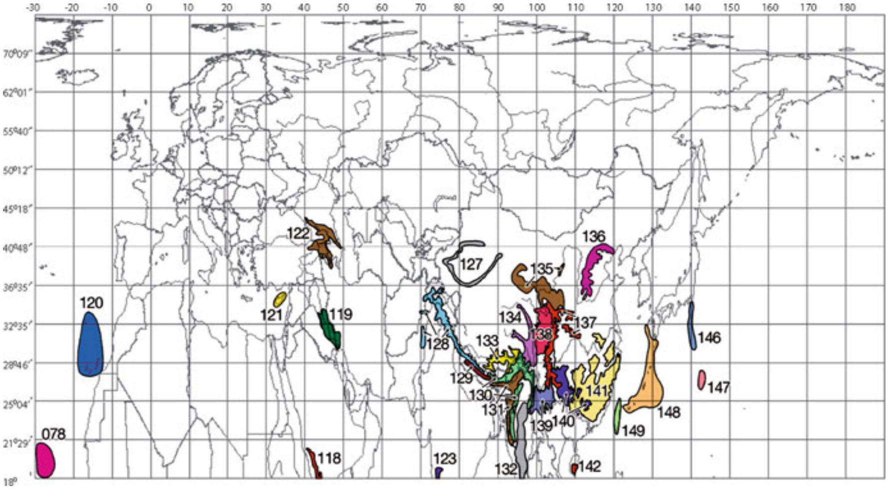

Fig. 9.6 Endemic Bird Areas as identified and codified by Stattersfield et al. (1998) and projected on our map of the Palearctic Region: (78) Cape Verde Islands, (118) South-west Arabian Mountains, (119) Mesopotamian marshes, (120) Canaries and Madeira, (121) Cyprus, (122) Caucasus, (123) western Ghats, (127) Taklimakan Desert, (128) Western Himalayas, (129) Central Himalayas, (130) Eastern Himalayas, (131) Assam Plains, (132) Irawaddy Plains, (133) Southern Tibet, (134) Eastern Tibet, (135) Qinghai Mountains, (136) Shaanxi Mountains, (137) Central Sichuan Mountains, (138) West Sichuan Mountains, (139) Yunnan Mountains, (140) Chinese subtropical forests, (141) South-east Chinese Mountains, (142) Hainan, (146) Izu Islands, (147) Ogasawara Islands, (148) Nansei Shoto, and (149) Taiwan

discriminate Cyprus from other areas (Fig. 9.3b, d). However, our Palearctic dataset analyzed for range-size rarity clearly marks Cyprus as a hotspot (Fig. 9.3c).

Lastly, we compare our results with two studies that focussed on Western Palearctic and European species of plants and terrestrial vertebrates, including birds (Humphries et al. 1999; Williams et al. 2000). For species richness, both studies found that the richest areas are in and around the mountain areas of central and southern Europe (Pyrenees, Alps, Carpathians, and Stara Mountains), whereas diversity is low in northern and southern Europe, particularly on the Iberian Peninsula. The pattern for range-size rarity was different, because the emphasis had shifted somewhat in that also hotspot regions were identified on the southern Balkan, and in Greece, and also in southeastern Spain, and on the islands of Mallorca, Corsica, Sardinia, and Crete. The results of these studies do more or less match our studies, particularly the results based on the Palearctic dataset. However, the hotspots of range-size rarity for our European dataset do not particularly match the range-size rarity results of these two studies (Humphries et al. 1999; Williams et al. 2000). This is because the index of range-size rarity for the 516 European songbirds discriminates only poorly between areas, particularly in Western Europe.

9.6 Conclusion

After visual inspection of the various results, we conclude that European hotspots of species richness are slightly more prominent in our Palearctic dataset as compared with our European dataset. But for the index of endemism, range-size rarity, there is a more pronounced difference between the hotspots identified by the Palearctic dataset and the European dataset. Basically, there is little or no differentiation in the European dataset. Therefore, we believe that our preliminary and qualitative analysis shows that it is important for hotspot and conservation studies to examine a natural biogeographic region, and not a geopolitical entity such as “Europe.”

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Chapter 10
Patterns and Hotspots of Carabid Beetle Diversity in the Palaearctic: Insights from a Hyperdiverse Invertebrate Taxon

Andreas Schuldt and Thorsten Assmann

Abstract With the rapid loss of biodiversity worldwide, understanding diversity distributions is central to develop efficient conservation strategies. However, current efforts such as the identification of biodiversity hotspots focus primarily on plants and vertebrates. To assess the generality of diversity distributions and hotspots derived from these taxa, we examine species richness and endemism patterns of carabid beetles as a hyperdiverse invertebrate taxon across the Palaearctic. The diversity of carabid beetles shows clear latitudinal dependencies, and centres of carabid diversity are located in southern Europe, Japan and southwest China. Richness and endemism distributions show a high degree of congruence with those of plants and amphibians across large parts of the Palaearctic. They also strongly covary with patterns of other invertebrates. Our results indicate that plant and vertebrate hotspots can also include high invertebrate diversity, with especially China qualifying as an outstanding Palaearctic hotspot of collective diversity. Similar environmental dependencies and strong effects of historical processes (i.e., long-term environmental stability) are probably key drivers of these common patterns. Our study extends the limited knowledge on invertebrate diversity distributions and helps to better understand general patterns in the spatial distribution of biodiversity.

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10.1 Introduction: Macroecology, Hotspots and Invertebrate Diversity

Invertebrate biodiversity by far exceeds the diversity of plants or vertebrates, with insects making up the largest part of total invertebrate species richness (Gaston and Hudson 1994; Stork 2007). They have been highly successful in populating most terrestrial and aquatic habitats on Earth. With the multitude of herbivores, detritivores, predators or parasitoids insects play essential roles in the functioning of ecosystems (Weisser and Siemann 2004). Although we are becoming increasingly aware of the important effects these taxa have in this respect, our knowledge about insect diversity and its spatial distribution at both large and small scales is insufficient (Lovell et al. 2007; Stork 2007). In order to obtain a deeper understanding of general patterns and drivers of biodiversity, however, it is crucial to strongly integrate these taxa into biogeographical research (Whittaker et al. 2005; Baselga 2008). This is also of importance for the development of adequate conservation strategies facing the worldwide and to a large part human-induced loss of biodiversity. Even though often not noticed, insects are heavily affected by species extinctions (Fonseca 2009). Most strategies, however, such as the identification of biodiversity hotspots, are based on data of plants or vertebrates, without adequate consideration of and information on invertebrates (Myers et al. 2000; Samways 2007; Fonseca 2009). This is often due to the insufficient availability of data on many invertebrate taxa concerning patterns over geographically extensive areas, which are of high interest for the general understanding of the spatial patterning of biodiversity (Lamoreux et al. 2006).

At coarser scale, however, the distribution patterns of several invertebrate taxa are fairly well documented over larger areas of several biogeographical regions (Hawkins et al. 2003; Wolters et al. 2006; Schuldt et al. 2009). Among them, carabid beetles (Coleoptera: Carabidae) stand out as a hyperdiverse insect taxon. Here, we synoptically review the present macroecological knowledge and provide new results on the diversity of this taxon to highlight the spatial patterns of hotspots in the Palaearctic realm. In contrast to other invertebrates, aspects of species richness and endemism distribution patterns as well as their covariation with the diversity of other taxa have been studied for carabids in detail across large parts of the Palaearctic (Schuldt and Assmann 2009; Schuldt et al. 2009; Schuldt and Assmann 2011). Taken together, these aspects provide extensive insights into diversity patterns that are, at present, unavailable for many other invertebrates.

Below, we discuss issues of data quality in the macroecological analysis of invertebrates, followed by an overview of broad-scale patterns of carabid beetle species richness and endemism and their potential environmental determinants in the Palaearctic. We then focus on cross-taxon congruence of diversity with vertebrates, plants and other invertebrates, assessing to what degree hotspots and conservation strategies derived from plant and vertebrate data (e.g., Myers et al. 2000) incorporate invertebrate diversity and how well carabids reflect diversity patterns of other invertebrates.

10.2 Carabid Beetles: Use and Limitations in Macroecological Studies

At the large scale we consider here, carabid beetles are one of the few and most diverse invertebrate taxa for which distribution patterns are fairly well documented across a large geographical area. Worldwide, almost 40,000 species have been described (Lorenz 2005), with about 11,000 known from the Palaearctic. Data are available for the whole Palaearctic from the comprehensive compilation by Löbl and Smetana (2003). However, as is the case for most invertebrates, spatially extensive diversity patterns can only be analyzed at a rather coarse scale (Baselga 2008; Schuldt et al. 2009). Insufficient documentation hinders reliable assignment of species data to fine-scaled or equal-area sampling units, which are often used in the analysis of the much better documented vertebrates or plants (cf. Jetz et al. 2008). For carabid beetles, country-level data are most accurate and were used in the analyses below, as many Palaearctic countries have a strong record of long-term faunal surveys. The data were extracted from Löbl and Smetana (2003). Even for vertebrates and plants, country-level data are frequently used for geographically extensive studies and have been shown to capture broad-scale diversity patterns of vertebrates, plants and invertebrates quite well (e.g., Kerr and Burkey 2002; Baselga 2008; Qian and Ricklefs 2008). Potential effects of country size were statistically taken into account in the analysis of carabid diversity patterns by including size as a covariable in partial correlation and regression analyses (Legendre and Legendre 1998). China was subdivided into its provinces and Russia was excluded, as a consistent subdivision of this large area was not possible. Analysis of species accumulation curves indicated that data quality is not equally good across the whole Palaearctic. Schuldt et al. (2009) showed that although species inventories for western Palaearctic countries have a high degree of completeness, eastern Palaearctic countries are in part less well sampled. For China we only have deficient data so far and during the last years, several hundreds of new carabid beetle species have been described from this region (Löbl and Smetana 2003). Of course, these differences in data quality need to be taken into account and thus diversity patterns were analyzed separately for the western and eastern Palaearctic and for China. Although it is possible to carefully evaluate general patterns and cross-taxon relationships with other taxa for the less well-sampled regions, results from the western Palaearctic are most reliable. In contrast, species inventories for vascular plants and vertebrates are much more advanced across the whole Palaearctic and species data can readily be retrieved from extensive compilations (see Schuldt et al. 2009 for a list of databases). In the cross-taxon comparison with carabid beetle diversity, amphibians and reptiles were selected as vertebrate representatives, as a consistent scale of analysis is difficult to achieve between low-mobile invertebrates and highly mobile birds or mammals (Grenyer et al. 2006).

10.3 Insights into Invertebrate Diversity Patterns: Carabid Beetle Diversity and Its Potential Determinants in the Palaearctic

Taken as a whole, Fig. 10.1a shows the bias in species richness of carabid beetles towards the western Palaearctic. However, the region-specific distribution patterns and centres of high species richness can be assessed when each subregion is examined separately. For the well-sampled western Palaearctic, a clear latitudinal gradient in species richness is evident ($R^2 = 0.42$; $p < 0.05$ for a curvilinear latitudinal regression model of species richness), with low richness in northern

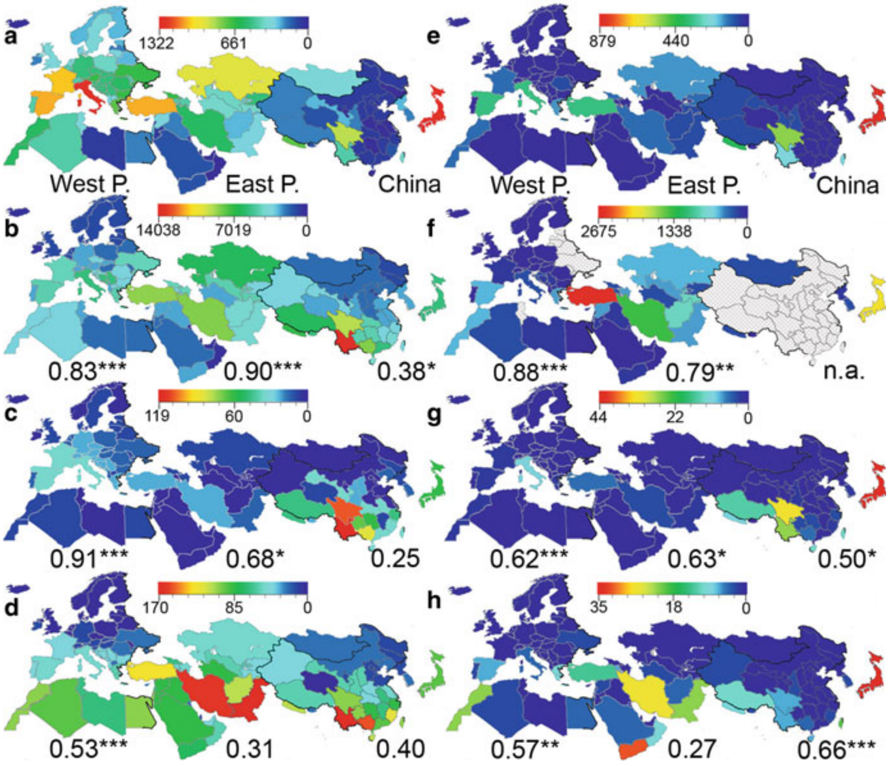

Fig. 10.1 Patterns of total species richness/endemism for **a**/**e**) carabid beetles, **b**/**f**) vascular plants, **c**/**g**) amphibians, and **d**/**h**) reptiles across the Palaearctic; based on data from Schuldt et al. (2009), reprinted with kind permission from John Wiley and Sons Publishers. Chequered countries were not included in the analyses (missing data for endemic plants in eastern Europe and China). Coefficients of correlation (partial correlations with area as covariable) with carabid beetle richness/endemism are given for plants, amphibians and reptiles for three separate subregions of the Palaearctic (based on carabid beetle data quality: western and eastern Palaearctic and China; region borders indicated by bold lines). Spatially corrected probabilities: ***$p < 0.001$; **$p < 0.01$; *$p \leq 0.05$ (after Dutilleul et al. 1993)

Europe and North Africa and highest species numbers in southern Europe (Fig. 10.1a). Similarly, carabid species richness in the eastern Palaearctic peaks at comparable latitudes, with Turkey and especially Japan as species-rich countries. For China, the south-western provinces Sichuan and Yunnan emerge as a region featuring a highly diverse carabid beetle fauna (Fig. 10.1a). Carabids are probably strongly undersampled in most Chinese provinces and the actual number of species in south-western China can be expected to be much higher (Schuldt et al. 2009), making this region one of the most diverse in carabid beetles in the whole Palaearctic.

Generally, the distribution of endemic carabids showed similar latitudinal patterns, with southern Europe, Japan and south-west China featuring highest numbers of endemic species in the three Palaearctic subregions (Fig. 10.1e). However, high endemic richness was more regionally restricted than total species richness and many countries had only few or no endemics at all. In the western Palaearctic, for instance, central and northern Europe is more or less devoid of endemic carabids.

With the well-documented carabid beetle data, the western Palaearctic is best suited for an assessment of the potential determinants causing the specific patterns in the current distribution of carabid beetle diversity. Relationships with environmental factors differed between widespread and endemic carabids (Table 10.1). Generally, broad-scale diversity patterns are considered to be driven by evolutionary and ecological processes which influence diversification, extinction or dispersal (Willig et al. 2003; Hillebrand 2004; Wiens and Donoghue 2004). For many taxa a strong impact of contemporary climatic conditions on current diversity distributions is assumed (e.g., Hawkins et al. 2003), but especially for dispersal-limited taxa historical processes may still play a more important role (Jetz et al. 2004; Araújo et al. 2008). Results for carabid beetles suggest that the strength of current climate versus historical effects might depend on dispersal abilities of the species (Schuldt and Assmann 2009). Species richness of widespread species in the western Palaearctic was strongly correlated with current climate (Table 10.1), primarily with variables related to ambient energy input (potential evapotranspiration, mean annual temperature; not shown). As widespread species, on average,

Table 10.1 Variation explained (% of total variation) by climate and topography in regression modelling for endemic, widespread and total species richness of carabid beetles in the western Palaearctic

	Endemic	Widespread	Total
Climate[a]	20.4	38.4	28.9
Topography[a]	36.3	17.0	25.8
Shared[b]	31.6	−1.5	4.0
Purely spatial	3.5	7.7	6.3
Total R^2	91.8	61.6	65.0
Probability	<0.001	<0.001	<0.001

Based on data from Schuldt and Assmann (2009)

[a] Independent and spatially structured effects

[b] Shared effects between (spatially structured) climate and (spatially structured) topography

make up about 90% of all species in the individual countries, the potential effect of climate also dominated the overall pattern of total carabid diversity. In contrast, the richness of range-restricted, endemic carabids (species with range sizes $<6 \times 10^5$ km^2; cf. Lumaret and Lobo 1996) was much less related to climatic variables and much stronger to topographic variability (measured as range in elevation) (Table 10.1). In part, topography might reflect habitat heterogeneity. However, its low impact on widespread as compared to endemic species, weak effects of climate on endemics and the absence of range-restricted species in large parts of central and northern Europe indicate that topography contains a strong historical signal (see also Schuldt and Assmann 2009). Topographic variability can enable survival of species during changes in climate (by enabling species to climb up or descend to suitable habitats) and promote isolation and diversification of species along altitudinal gradients of temperature and other environmental conditions (Hewitt 1999; Jetz et al. 2004). Pleistocene glaciations probably played a major role in this respect in the western Palaearctic (Hewitt 1999; Araújo et al. 2008), with dispersal-limited carabids hindered in their recolonization of central and northern Europe after the retreat of the ice shield and permafrost soils. This becomes especially clear when considering distribution patterns of carabid beetles adapted to below-ground habitats. Due to their specific habitat requirements and morphological adaptations, these species are strongly limited in their dispersal (Assmann et al. 2010). Despite the availability of suitable habitats, central and northern Europe largely lack subterranean carabid beetle species (Schuldt and Assmann 2011). High diversity of these taxa can only be found in mountainous southern regions of the western Palaearctic, which offered environmentally favourable conditions over long periods and long-term opportunities for diversification (Assmann et al. 2010; Schuldt and Assmann 2011).

Differences in patterns and determinants of diversity between widespread and range-restricted species can have important implications for our understanding of general biodiversity patterns and of the mechanisms behind these patterns. Moreover, these differences can be relevant also for biodiversity conservation. Many invertebrate taxa are characterized by low dispersal power and conservation strategies neglecting invertebrates and focusing only on vertebrates or plants might miss an important part of biodiversity if distribution patterns of species richness or endemism differ between these taxa.

10.4 Biogeography and Diversity Hotspots: Congruence Between Invertebrates, Vertebrates and Plants?

Conservation strategies are often based on well-known vertebrates or vascular plants, especially at larger scales (Myers et al. 2000; Lamoreux et al. 2006). Identifying hotspots of highest diversity has been one of the successful strategies in allocating funding to regions of high conservation priority at continental and global scales (Myers and Mittermeier 2003). However, there is little information to what degree diversity patterns of vertebrates and plants reflect those of invertebrates and whether hotspots derived from patterns of the former taxa also incorporate high invertebrate diversity (Whittaker et al. 2005; Samways 2007). Several attempts have been made to compare these patterns over larger geographic areas, however, with varying results (e.g., Gaston and David 1994; Balmford and Long 1995; Pearson and Carroll 1998). Further studies are needed to get a clearer picture of general patterns in the distribution of biodiversity. The data for carabid beetles from such a large area as the Palaearctic offer an excellent opportunity to assess the congruence between a highly diverse insect taxon and phylogenetically unrelated vertebrates and plants. In contrast to other taxa, data on both species richness and endemism are available, which additionally allow to test if overall centres of richness and endemism can be identified.

Both total richness and endemism of carabid beetles showed high and significant correlations with species richness and endemism of vascular plants and amphibians across large parts of the Palaearctic (partial correlation coefficients with country area as a covariable ranged from 0.91 to 0.62; Fig. 10.1). Reptile diversity patterns deviated from those of the other taxa and correlations with carabids were lower, with highest reptilian richness in more southern regions of both the western and eastern Palaearctic. Reptiles are known for their strong physiological dependence on energy input (Rodriguez et al. 2005), which explains their high diversity in the most southern parts of the Palaearctic. Plant, amphibian and also carabid diversity are more strongly related to the water–energy balance, increasing with available energy only as long as water availability does not become limiting (Rodriguez et al. 2005; Kreft and Jetz 2007; Schuldt et al. 2009). Similar environmental dependencies might explain the high correlations between broad-scale richness patterns of these taxa (Hawkins et al. 2003; Willig et al. 2003). Although richness patterns of amphibians and plants were also highly correlated across China (Pearson's $r = 0.85$; $p < 0.01$), correlations with carabid richness in China were weak for both amphibians and plants (Fig. 10.1b, c). However, this is due to the deficient data for carabid beetles in most of the Chinese provinces. Much higher numbers of species can be expected for most of these provinces, suggesting that cross-taxon correlations with plants or amphibians could become stronger with more complete datasets (Schuldt et al. 2009). Despite the evident undersampling of carabids, correlations between endemism patterns of both vertebrate taxa and carabids were fairly high across China (Fig. 10.1g, h). We lack reliable data for endemic plants in many provinces. However, extremely high numbers of endemic plants for the south-western provinces Yunnan and Sichuan, which also belong to the provinces with highest numbers of endemics of the other taxa, indicate that patterns and especially endemism hotspots are probably comparable (Myers et al. 2000; Tang et al. 2006).

In general, plants, amphibians and also reptiles feature a high number of range-restricted taxa with low dispersal abilities (Araújo and Pearson 2005), a pattern similar to carabids. As for carabids, patterns of endemicity of plants, amphibians and reptiles have thus probably been strongly influenced by historical processes (such as glaciation events), which leads to high congruence in endemic richness distributions across the Palaearctic (Jansson 2003; Araújo et al. 2008). In the western Palaearctic, these patterns are also congruent with the so-called “Massifs de refuge”, areas considered the glacial refugia of many taxa and harbouring a high diversity of both endemic plants and insects (Holdhaus 1954; Habel and Assmann 2010).

Thus, although not necessarily the most species-rich regions for all taxa (especially due to deviating patterns of reptiles), centres of collective diversity combining high species richness and endemism of all four taxa can be determined at this coarse scale (see also Gaston and David 1994). For the well-sampled western Palaearctic, Italy, Greece and Spain are identified as collective hotspots of high plant, vertebrate and invertebrate diversity (Table 10.2). Even though less well-sampled for carabids, Japan, Turkey and especially south-west China emerge as eastern Palaearctic diversity hotspots, which include high richness and endemism of carabid beetles (Table 10.2, Fig. 10.1). Southern Europe and south-west China are well known as two of the most important global hotspots, especially of plant diversity (Myers et al. 2000). The results for carabids show that such hotspots can also include a large proportion of the diversity of invertebrate taxa (see also Gaston and David 1994; Lumaret and Lobo 1996). In this respect, China (and especially its south-western part) qualifies as a prominent Palaearctic centre of diversity for which further biodiversity research and conservation efforts are urgently needed (Soutullo et al. 2008). Even with the incomplete data available today, China harbours at least one quarter of all carabid species known at present from the Palaearctic and many of these species have been recorded so far only from the extremely biodiverse regions of south-west China (Löbl and Smetana 2003). Considering the steep increase in new species being recorded from China, the actual number is likely to be much higher, underlining the importance of China

Table 10.2 Species numbers (total and endemic) of carabid beetles, vascular plants, reptiles and amphibians in hotspot regions of the Palaearctic, arranged after hotspot regions defined by Myers et al. (2000)

		Carabid beetles		Vascular plants		Reptiles		Amphibians	
	Area (10^3 km^2)	Total	Endemic (% of total)	Total	Endemic (% of total)	Total	Endemic (% of total)	Total	Endemic (% of total)
Mediterranean hotspot									
Greece	130.8	714	158 (22.1%)	4,992	419 (8.4%)	64	8 (12.5%)	22	3 (13.6%)
Italy	294.0	1,273	325 (25.5%)	5,598	252 (4.5%)	53	4 (7.5%)	37	11 (29.7%)
Spain	499.5	1,086	320 (29.5%)	5,048	537 (10.6%)	53	7 (13.2%)	33	3 (9.1%)
Turkey	770.8	1,086	318 (29.3%)	8,579	2,675 (31.2%)	130	13 (10.0%)	26	7 (26.9%)
South-east Asian hotspots									
Taiwan	32.3	392	209 (53.3%)	3,526	1,067 (30.3%)	101	19 (18.9%)	35	16 (45.7%)
Nepal	143.2	697	400 (57.4%)	6,973	315 (4.5%)	113	9 (8.0%)	46	10 (21.7%)
Japan	374.7	1,322	879 (66.5%)	5,372	2,000 (37.2%)	97	35 (36.1%)	56	44 (78.6%)
Yunnan	436.2	458	223 (48.7%)	14,038	n.a.	170	6 (3.5%)	119	27 (22.7%)
Sichuan	569.0	844	527 (62.4%)	9,314	1,467 (15.8%)	99	6 (6.1%)	103	32 (31.1%)

Based on separate partial (area included as covariable) principal components analyses (PCA) for the western and eastern Palaearctic and for China

n.a.: no endemic plant data available for Yunnan for invertebrate diversity, documented also from studies of other taxa (e.g., Cassola and Pearson 2000; Foley et al. 2007).

Of course, carabid beetles are just one, even though extraordinarily species-rich, invertebrate taxon. Are the broad-scale diversity patterns of carabid beetles representative of other invertebrates? This is difficult to assess for the entire Palaearctic, as species richness distributions of many other taxa are even less well documented than those of carabids in the eastern parts of this region. However, at least for the western Palaearctic and especially for Europe comprehensive data for various invertebrate taxa have accumulated over the last decades (Van Swaay and Warren 1999; Fauna Europaea Web Service 2004; Foley et al. 2007; Baselga 2008; Finch et al. 2008; Pautasso and Fontaneto 2008; Schlick-Steiner et al. 2008; Pautasso and Powell 2009; Ulrich and Fiera 2009). Species richness of many taxa has been shown to be related to similar environmental effects as total carabid species richness, indicating that broad-scale richness distributions might show similar patterns (e.g., Hawkins et al. 2003; Baselga 2008; Keil et al. 2008). And in fact, species richness patterns of different invertebrate taxa, extracted from recent biodiversity studies (Fig. 10.2), are highly correlated with carabid richness across European countries. Partial correlations (with country area included as a covariable and corrected for spatial autocorrelation according to Dutilleul et al. 1993) range from about 0.6 (mosquitoes: Pearson's $r = 0.57$; $p = 0.015$) to more than 0.9 (spiders: $r = 0.91$; $p < 0.001$; ants: $r = 0.92$; $p < 0.001$). Only aphids, for which species radiations in temperate regions are being assumed (Ortiz-Rivas et al. 2004), show weak correlation with carabid diversity ($r = 0.33$; $p = 0.20$). Highest richness of all other taxa is located in southern European regions. And even though regions with highest taxon-specific diversity are not necessarily identical for all taxa (as was also observed above for the relationships between carabids and, for instance, reptiles), the collective hotspots identified for carabids, vertebrates and plants are also very rich in species of other invertebrates (Fig. 10.2; Schuldt and Assmann 2010). Thus, hotspots based on broad-scale carabid beetle data might indeed capture high species richness of many other invertebrates, at least across the Palaearctic.

10.5 Many Questions Remain: Challenges in Invertebrate Macroecology

There are many aspects of invertebrate diversity distributions that we are unable to address in detail in our study and with the data that are currently available for most invertebrates. How do the patterns we observed fit into global hotspot research? Our study is restricted to the Palaearctic, comprising mostly boreal, temperate and subtropical regions. Highest biodiversity of many taxa can be found in the tropics, but reliable data from these regions are only available for few and comparatively species-poor invertebrate taxa (Balmford and Long 1995; Stork 2007). Global

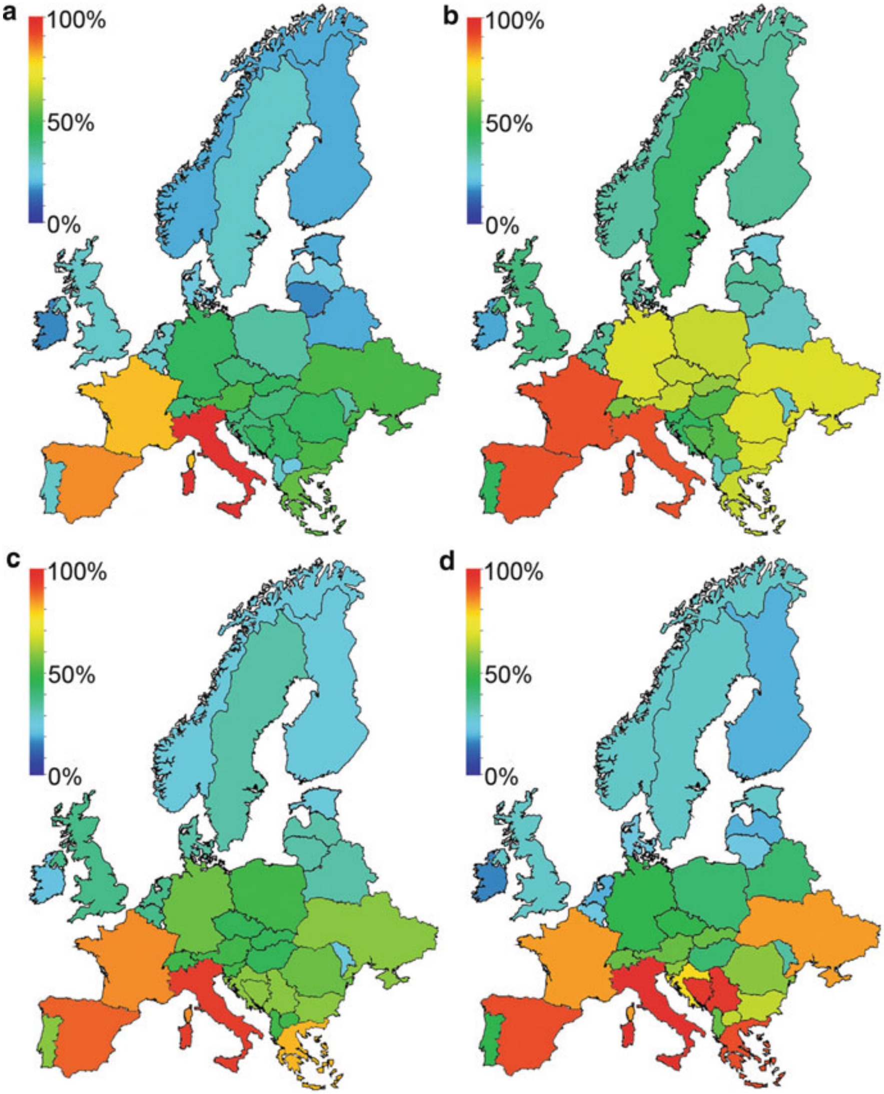

Fig. 10.2 Patterns of species richness for (**a**) carabid beetles, (**b**) other invertebrates (mean values averaged over spiders, springtails, dragonflies, mayflies, stoneflies, aphids, ants, mosquitoes, caddisflies, butterflies and longhorn beetles), (**c**) vertebrates (mean values averaged over mammals, amphibians and reptiles), and (**d**) vascular plants across Europe. *Colours* indicate the proportion of species each European country represents in relation to the country in which the highest country-level richness (=100%) of the respective taxon was recorded (e.g., Germany has about half as many carabid species as Italy, the most species-rich country). Data assembled from Van Swaay and Warren (1999); Fauna Europaea Web Service (2004); Foley et al. (2007); Baselga (2008); Finch et al. (2008); Pautasso and Fontaneto (2008); Schlick-Steiner et al. (2008); Pautasso and Powell (2009); Schuldt et al. (2009); Ulrich and Fiera (2009)

datasets are available for, e.g., tiger beetles (Cassola and Pearson 2000) and mosquitoes (Foley et al. 2007), but even these taxa still show a strong increase in species number in regions such as the Neotropics or south-east Asia (Cassola and Pearson 2000). Balmford and Long (1995) studied cross-taxon congruence of range-restricted birds with richness of tiger beetles and papilionid butterflies across more than 100 tropical countries. They found low correlations with total species richness of these insects, but fairly high congruence with numbers of endemic species. Whether such relationships also hold for such highly diverse taxa as carabids would be important to know for global conservation strategies, but is difficult to assess based on the presently available data. However, the results of our study provide important insights in this respect. With an improvement of data quality (regarding more comprehensive data at finer scales as well as new descriptions of species) also for the Palaearctic, the scale dependence of the observed patterns for carabids could be assessed. Mechanisms determining diversity patterns at more local scales can differ from those at larger scales and often, cross-taxon correlations of diversity are much weaker at such local scales (Whittaker et al. 2001; Wolters et al. 2006). Although broad-scale studies might thus be limited in their utility for actual reserve selection, they are of particular interest in understanding general patterns of overall biodiversity and can help guide conservation decisions at regional and global scales (Myers et al. 2000; Lamoreux et al. 2006).

Species richness and endemism are two of the most commonly used measures of biodiversity, but of course, further aspects of diversity such as the spatial turnover in species (beta diversity) need to be taken into account in future studies. The analysis of endemism patterns only partially addresses such questions of changes in species composition, showing the uniqueness of faunal elements (i.e., of endemic species) for the single countries of the Palaearctic.

Our results from the broad-scale study of carabid beetle diversity can only partly address the many aspects concerning invertebrate diversity distributions. However, they provide important insights into the insufficiently studied spatial patterning of invertebrate diversity over a geographically extensive area and its potential environmental determinants. Our study helps to put results primarily derived from the study of vertebrates and plants into a broader perspective, incorporating a larger range of the world's biodiversity than usually considered.

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Chapter 11
The Carpathians as a Major Diversity Hotspot in Europe

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Abstract The Carpathians are one of the major mountain ranges of Europe, but still one of its least studied regions. It is increasingly recognized that they played a major role in the formation and Pleistocene survival of numerous continental, arctic, and arctic–alpine taxa. Many endemic taxa have been described from these

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mountains. The number of phylogeographic/phylogenetic studies covering at least partially the Carpathians is also increasing. These studies reveal unevenly distributed genetic and taxonomic diversity. In this work, we analyse population genetic structures in the Carpathians revealed by case studies on aquatic insects, comparing them to existing literature data on plants, butterflies, vertebrates, and the distribution of several microendemics. The distribution of molecular lineages and/or microendemics show strong biogeographic structures within the Carpathians. The overlap between the distribution barriers of microendemics and intraspecific molecular lineages suggests that isolation of populations among the major Carpathian ranges (Western Carpathians, Eastern Carpathians, Apuseni Mts, Southern Carpathians, Banat and Serbian Carpathians) played a major role in promoting Carpathian diversity.

11.1 Introduction

Identifying and mapping biodiversity "hot spots" is of major interest in both basic biological research and applied research for conservation and management of natural habitats. This is particularly true, since awareness and acknowledgment of the global biodiversity crisis have spread within the scientific community and beyond. Regional genetic diversity may be very important for the long-term survival of many organisms, and is thus directly relevant to species and habitat conservation (Frankham 1995). Phylogeographic surveys can therefore have major implications for conservation, e.g., by identifying genetically diverse populations or communities (evolutionary significant units – Avise 2005), and/or identifying potential future refugia of this diversity (Crandall et al. 2000; Hickerson et al. 2010). Furthermore, assessing genetic diversity in fragmented landscapes among populations or between sister taxa may contribute to uncovering cryptic biodiversity that is often ignored in conservation strategies (Moritz and Faith 1998).

It is widely accepted that the Central European Mountains harbor a major component of biological diversity in Europe. Pleistocene glacial cycling has received a lot of attention in recent studies as a motor driving differentiation and diversification processes in the Central European flora and fauna (see e.g., Hewitt 2004; Schmitt 2007 for reviews). The results of numerous surveys (e.g., Hewitt 1996; Schmitt and Seitz 2001; Ursenbacher et al. 2006) have greatly improved our understanding about the role of the Mediterranean peninsulas in the glacial survival of numerous temperate taxa, but also about the present distribution of biodiversity in several extra-Mediterranean refugia (e.g., the Alps, the Central European Highlands, or the Carpathians, see Kotlík et al. 2006; Magri et al. 2006). The majority of existing studies focus on terrestrial species, but recently more aquatic organisms have been subject to analysis (e.g., Pauls et al. 2006; Sedivá et al. 2008). From these studies, we know that cold-tolerant aquatic species survived the glaciations in the vicinity of ice sheets due to the greater thermal stability and buffering capacity of aquatic environments. This may be the source of high levels of genetic diversity of aquatic insects in the freshwaters of the Central European Mountains.

The Carpathians (Fig. 11.1) deserve special attention due to their particular historical, biogeographical and ecological features. This region is an area of sympatry for organisms of different biogeographic origin and constitutes a true

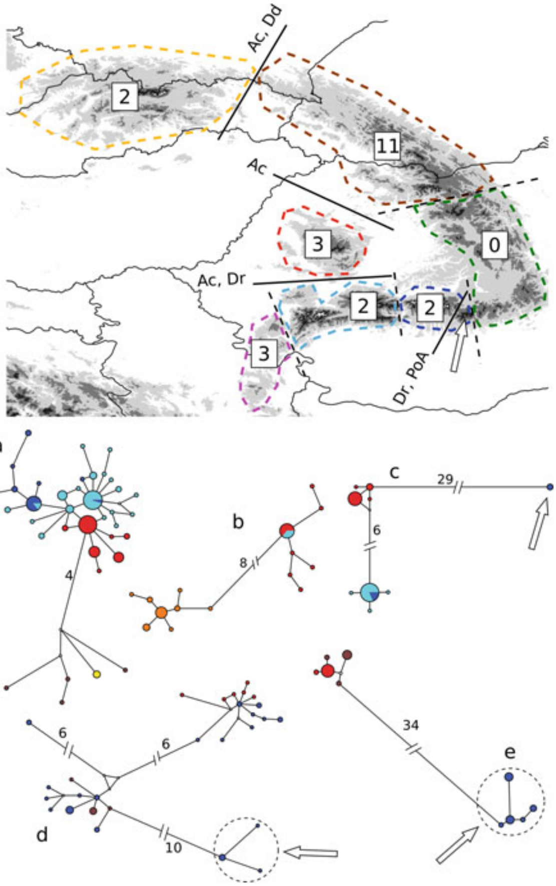

Fig. 11.1 Major ranges of the Carpathians: *yellow*: Western Carpathians; *brown*: northern region of the Eastern Carpathians; *green*: southern region of the Eastern Carpathians; *blue*: eastern region of the Southern Carpathians; *turquoise*: western region of the Southern Carpathians; *pink*: Banat and Serbian Carpathians; *red*: Apuseni Mts. *Arrows* mark the Bucegi Mts and its endemic lineages. *Dashed lines* on map represent important barriers identified only by the distribution of species endemic to one or more Carpathian regions; continuous lines represent barriers identified both by identified genetic lineages and the distribution of endemic species. Numbers over major Carpathian regions present the number of Trichoptera species endemic to those regions. Species with distinct lineages are shown next to the gene flow barriers. Numbers over connecting lines of the median joining networks show the number of nucleotide differences between disjunct lineages. *Ac Arcynopteryx compacta* (a), *Cm Chaetopterygopsis maclachlani* (b), *Dd Drusus discolor*; *Dr Drusus romanicus romanicus* (c), *PoA P. occulta*, species A (d), *PoB Pedicia occulta*, species B (e)

reserve of the native European biodiversity (e.g., Varga 2003; Kotlík and Berrebi 2001; Ursenbacher et al. 2006). Despite the similarities with the Alps, the Carpathians are unique in many ways due to their particular geography and ecological complexity. Several areas with high biodiversity have been already identified here with numerous endangered or endemic species (see e.g., Botoşaneanu 1975; Kis 1980). The role of the Carpathians as glacial refugia is increasingly recognized (e.g., Kotlík et al. 2006; Sedivá et al. 2008; Provan and Bennett 2008; Schmitt 2009). Forest patches existed in the Carpathians throughout the Würm glaciation (Feurdean et al. 2007; Schmitt and Haubrich 2008). The existence of forest patches confirms the presence of habitats with favorable microclimate in otherwise unsuitable areas.

However, the Carpathians, as well as the whole Balkan Peninsula, have received less attention from phylogeographers than other parts of Europe. Even basic faunistic/floristic resources are scarce for numerous taxa. The diversity of these mountains is especially valuable as they are relatively unimpacted by human activities compared to many areas in Iberia and Italy.

The current notion that multiple glacial refugia exist in the Carpathians is based on the existence of microendemics, but molecular case studies are rare. However, a number of surveys focusing on more widely distributed mountain aquatic insects have been carried out in the last few years (e.g., Lehrian et al. 2010; Pauls et al. 2006, 2009; Ujvárosi et al. 2010). These studies provide first information about the extent of cryptic diversity and divergence patterns of the Carpathians.

The present work analyses and reviews the results of eight case studies on mountain aquatic insects. The available data is rather low-resolution with respect to the Carpathians, as these studies often focused on continent-wide distributed species. However, the accumulated information suggests some general patterns of the Carpathian genetic diversity. The patterns show important similarities with the biogeographic patterns and/or genetic structures of other endemic and widespread terrestrial and aquatic taxa. Our main objective is to identify general trends in the diversification of aquatic species in the Carpathians and to compare these with the distribution patterns of microendemic taxa.

11.2 Materials and Methods

We reanalyzed mitochondrial *COI* datasets from seven phylogeographic case studies (Bálint 2008; Bálint et al. 2011; Lehrian et al. 2010; Pauls et al. 2006, 2009; Theissinger 2011, Ujvárosi et al. 2010) of mountain aquatic insects with special focus on the Carpathians. Sequences from Carpathian individuals used in these surveys were aligned using BioEdit (Hall 1999). Haplotypes were identified in DnaSP v.5 (Rozas et al. 2003). The relationships of haplotypes were analyzed using median-joining networks in Network v.4.516 (Bandelt et al. 2010).

The geographic structuring of populations and potential barriers of gene flow were analyzed individually for species with at least three sampling sites using spatial analysis of molecular variance (SAMOVA, Dupanloup et al. 2002). The method defines group composition in which populations within a group are as genetically homogeneous as possible (minimized F_{SC}) and groups are maximally differentiated (maximized F_{CT}). The analysis was run for groups $k = 2$ to $k = n-1$ (where n is the number of sampled populations). The significance of fixation indices was tested by 100 permutations.

11.3 Results of the Molecular Case Studies

Arcynopteryx compacta (McLachlan 1872) is a widespread stonefly with a Holarctic distribution. The populations sampled in the Rodnei, Tatra, Făgăraş, Retezat and Apuseni Mts show remarkable population genetic structure within the Carpathians (Fig. 11.1a, Theissinger 2011). Although the species was previously recorded from a few sites in the southern Eastern Carpathians, we could not include samples from this area. Western and northern Eastern Carpathian haplotypes are grouped together. They are completely separated from the Apuseni Mts and Southern Carpathian populations by a relatively deep split (4 bp), sharing no common haplotypes. This indicates complete lineage sorting despite small interregional genetic distances. The three most common haplotypes identified belong to the Apuseni Mts, and eastern and western Southern Carpathian populations, respectively. There are only a few shared haplotypes between the eastern and western regions of the Southern Carpathians. The results show at least two diversity centres for this species, one in the Western and northern Eastern Carpathians, and one for the Apuseni Mts and the Southern Carpathians. These lineages are also separate from Eastern Alps and Balkan lineages of the species (Theissinger 2011). The SAMOVA supports the existence of gene flow barriers between the Western Carpathians and the northern Eastern Carpathians, the northern Eastern Carpathians and the Apuseni Mts, and between the Apuseni Mts and the Southern Carpathians.

Chaetopterygopsis maclachlani Stein 1874 is a widespread Palaearctic caddisfly that occurs from the Pyrenees to the Baikal (see e.g., Lehrian et al. 2010). The larvae of the species are remarkably specialized on aquatic *Fontinalis* mosses and inhabit moss beds in mountain streams. An endemic sister species, C. *sisestii* Botoşaneanu 1961 is also present in the Carpathians. The samples of *C. maclachlani* that we discuss here were collected in the Western Carpathians, the Apuseni Mts and the western Southern Carpathians (Lehrian et al. 2010). Sporadic records exist in the Eastern Carpathians, but recent efforts to sample populations from there were not successful.

The most important split concerning all the investigated European populations is located between the Western and the Southern Carpathians, somewhere in the Eastern Carpathians. The Western Carpathian lineage is strongly divergent from those found in the Apuseni Mts and the Southern Carpathians, with no shared haplotypes (Fig. 11.1b). There are a number of unique haplotypes found in the Apuseni, and the most abundant haplotype is shared with the Southern Carpathians. The Apuseni and Southern Carpathian populations share haplotypes with the Rila and the Rhodopes (Lehrian et al. 2010). The Western Carpathian lineage of *C. maclachlani* is rather similar to other Central European lineages (especially those from the Black Forest, Vosges, Sudety Mts, Pfaelzer Wald). The existing data suggest a more continuous range of this species in Central Europe during the last glacial maximum (LGM), with ongoing lineage sorting (Lehrian et al. 2010). Due to our sampling gap in the Eastern Carpathians, we were not able to identify the exact location of an Eastern Carpathian gene flow barrier with SAMOVA.

Drusus discolor (Rambur 1842) is another widespread European caddisfly, present in almost all the mountains of Europe. It has a patchy distribution and highly fragmented population genetic structures (Pauls et al. 2006). The species inhabits fast-flowing mountain streams and is widely distributed throughout the Carpathian arc, missing only from the Apuseni Mts. The Carpathian populations show a heterogeneous genetic structure, with unique haplotypes in the Western Carpathians, the northern regions of the Eastern Carpathians, and in the eastern areas of the Southern Carpathians. A central haplotype is shared among all Carpathian ranges, indicating recent or ongoing gene flow. Existing data indicate the glacial survival of the species in at least two differentiation centres (for more details see Pauls et al. 2009). The SAMOVA supports a gene flow barrier between the Tatra and the northern Eastern Carpathians.

Drusus romanicus Murgoci and Botoşaneanu 1953 is a sister species of *D. discolor* with a more restricted distribution. The taxon is split into two genetically and morphologically distinct subspecies, one endemic to the Carpathian Mts (*D. r. romanicus*), the other to the Balkan Peninsula (*D. r. meridionalis*). The ecological requirements of the two species are indistinguishable. Although both species are present in the Southern Carpathians, it is rare to find them in sympatry in the same stream valley (Pauls et al. 2009). *Drusus romanicus* completely replaces *D. discolor* in the Apuseni Mts but is missing from the entire Eastern and Western Carpathians. The species shows remarkable population genetic structure in the Carpathians, with three highly divergent lineages (Fig. 11.1c). One of these is endemic to the Apuseni Mts, another to the Southern Carpathians, and a third to the Bucegi Mts, the easternmost massif of the eastern Southern Carpathians. There are no shared haplotypes among these ranges. The Bucegi lineage is different in 29 nucleotides from the most similar haplotypes of *D. r. romanicus*, but it is closer to *D. discolor* haplotypes. This might indicate an old introgression as a result of a rare interspecific hybridization event between the two species, with current reproductive isolation, or the existence of a cryptic species in the Bucegi (Pauls et al. 2009). The SAMOVA supports the existence of a gene flow barrier between the Apuseni Mts and the Southern Carpathians, and also the isolation of the Bucegi from the rest of the Southern Carpathians.

Rhyacophila tristis Pictet 1834 belongs to a Euromediterranean species group sensu Bănărescu (1991). The species is widespread in Europe with a distribution similar to *D. discolor*. The species is present in fast-flowing mountain streams located at various altitudes. The larvae have no gills, thus survival is most probably strongly influenced by dissolved oxygen concentrations. Populations collected from all regions of the Romanian Carpathians are genetically diverse, but without apparent geographic structures. The lineages identified are, however, endemic to the Carpathians and they are strongly divergent from Alpine and Balkan lineages (Bálint et al. 2011). In-situ glacial survival of the Carpathian populations seems plausible, but without apparent lineage sorting among the distinct Carpathian ranges. However, the results should be interpreted with caution, as the large number of singleton haplotypes, i.e., haplotypes carried only by single individuals, indicates insufficient sampling. The SAMOVA does not indicate the presence of a gene flow barrier.

Rhyacophila carpathica (Botoşaneanu 1995) is a member of the *R. tristis* species group. Morphometric and genetic analyses suggest that the species was separated from *R. aquitanica* (present in the Massif Central, Vosges, Black Forest and Southern Alps) due to an ancient allopatric differentiation event (Bálint et al. 2008, 2009). The species is entirely restricted to the western ranges of the Southern Carpathians. *Rhyacophila carpathica* and *R. tristis* are often found in the same streams, but in different sections of the stream: the former species inhabits springs and headwaters (Crenal to Epirhithral), whereas the latter is regularly found further downstream (Epirhithral to Hyporhithral). Morphometric analyses of the male genitalia of *R. carpathica* suggest characteristic differences in all mountains in the western Southern Carpathians (Bálint et al. 2008). However, a genetic study using *COI* sequences (mtDNA) found only a few haplotypes (Bálint 2008). These show a peculiar distribution: a single common haplotype is present in all the sampled Carpathian populations. Relatively divergent haplotypes were found in a single, high-altitude population of the species in the Retezat Mts, indicating that *R. carpathica* most probably underwent a postglacial range expansion starting from this mountain. The SAMOVA did not identify any gene flow barriers within the range-restricted species.

Pedicia occulta (Meigen 1830) is a large cranefly species with a Euromediterranean distribution sensu Bănărescu (1991). It is present in all parts of Europe including many islands of the Mediterranean Sea and extends east to the Caucasus. The species is missing from Fennoscandia. Based on morphometric characters and *COI* (mtDNA) markers genetically distinct morphotypes of the species were delimited (Ujvárosi et al. 2010). These morphotypes were formed after an ancient speciation event (the molecular clock approach using a conventional 2.3% sequence divergence/mys suggests a 24 million year old split). Both morphotypes are present in springs and headwaters and often occur in sympatry. The larvae are carnivorous and live in stream moss beds.

Species "A" of *P. occulta* is a widespread species. It shows remarkable genetic diversity in the Carpathians (Fig. 11.1d). Three haplotypes were entirely endemic to the Bucegi Mts. These are genetically distant from the other lineages. The observed strong structures of the other lineages are not confined to specific mountain ranges. The extent of differentiation suggests recent secondary contact among several populations that developed in isolation over a longer period as an effect of possible glacial separation. Besides confirming high genetic diversity and distinguishing the endemic Bucegi lineage, no further conclusions can be made due to the limited sampling of individual populations as suggested by the number of singletons. In addition to the Carpathian material, only a few populations of species A from Bulgaria were analyzed with genetic methods. These suggest a shallow divergence between the Bulgarian mountains and non-Bucegi Carpathian material (Ujvárosi et al. 2010). However, over 250 specimens from the entire distribution range of species A were analyzed morphometrically and these specimens seem to be homogeneous regarding the measured genitalia and wing characters. The SAMOVA shows the existence of a gene flow barrier between the Bucegi Mts and the rest of the Southern Carpathians.

Species “B” of *P. occulta* is restricted to the northern range of the species. The species was recovered almost exclusively from the Carpathians, but a single population with similar characters was also found in the Alps (Ujvárosi et al. 2010). The specimens analyzed for *COI* (mtDNA) variability were collected in the northern Eastern Carpathians, in the Apuseni Mts, and in the eastern Southern Carpathians (Bucegi Mts). The genetic structure shows strong similarities to those of *D. romanicus* (Fig. 11.1e). All haplotypes are unique to different Carpathian ranges. Interestingly, the northern Eastern Carpathian samples are closely related to those from the Apuseni Mts, suggesting a rarely observed connection otherwise known from the woodland ringlet butterfly, *Erebia medusa* (Schmitt et al. 2007). The Southern Carpathian sequences (obtained from the Bucegi Mts) are again highly divergent from the other haploypes, as in species A. The differences between these two groups exceed 7% sequence divergence, suggesting cryptic allopatric speciation events, pre-dating the LGM. The morphometric measurements did not reveal differences between these two apparently distant clades, as was the case for lineage A. These characters might be under stabilizing selection. The number of populations sampled was too low to infer conclusive details about the location of gene flow barriers using SAMOVA.

11.4 Patterns of Endemism in the Carpathians

According to Varga (2003), the majority of Carpathian terrestrial endemics are flightless or short-winged species. However, numerous endemic species and subspecies (often with well-developed wings) can be found among insects with aquatic life stages, probably the best examples being the caddisflies (50 endemic taxa of 299, Graf et al. 2008) and the stoneflies (13 endemics of 131, Graf et al. 2009). In contrast, endemic Lepidoptera species are comparatively rare in the Carpathians, and most are Microlepidoptera with poor dispersal capacity (Varga 2003). Endemism of Macrolepidoptera is more characteristic on the subspecies level (e.g., subspecies of *Erebia*, see Varga 2001). The endemic species or subspecies are often spread over several ranges of the Carpathians, and some of them are present throughout the entire mountain chain. The distribution patterns of those species restricted to one or several mountains exhibit notable similarities with the distribution of genetic lineages of the analyzed aquatic insects (Table 11.1, Fig. 11.1).

Several Carpathian endemics are present on more than one mountain. The distribution of these species has strong similarities with the microendemics, or the molecular lineages revealed in the aquatic case studies. Populations of numerous taxa with wider distribution in Europe often have two or more lineages in the Alps (Schmitt 2009) and the same is true for the Carpathians: at least two distinct genetic lineages are present for *C. maclachlani*, *A. compacta*, *D. discolor*, *D. romanicus*, and both *P. occulta* species. These lineages most probably correspond with independent glacial refugia (e.g., Babik et al. 2005 – *Lissotriton vulgaris* and *L. montandoni*, Schmitt et al. 2007 – *Erebia medusa,* Hofman et al. 2007 – *Bombina variegata*). Schmitt (2009) reviews several European mountain taxa that have multiple genetic lineages within a single mountain range. The genetic distance among these lineages can be very large, often suggesting cryptic species. Similar patterns of very high genetic differentiation within morphologically homogeneous taxa were revealed in the Carpathians for *D. romanicus* and *P. occulta* species B. The ancestors of these organisms probably diverged prior to the Pleistocene and the lineages evolved independently in geographic isolation. Similar patterns of Pre-Pleistocene divergence have been reported on the Balkan peninsula for *Mesotriton alpestris* (Sotiropoulos et al. 2007) and endemic Drusinae (Previsić et al. 2009).

The major diversity centres of the Carpathians are characterized by numerous microendemics. The genetic population structure of the analyzed aquatic insects corresponds well with the distribution patterns of endemic taxa, and thus the location of important geographic barriers that promote isolation of lineages (Fig. 11.1, Table 11.1).

The Apuseni Mts are bordered by the Someş river in the north and the Mureş river in the south. The aquatic insects *A. compacta* and *D. romanicus* both have distinct lineages in these mountains (Fig. 11.1a,c). Rafiński et al. (2001) show that the genetic lineage characterizing the Transylvanian endemic subspecies of the smooth newt (*Lissotriton vulgaris ampelensis*) had glacial refugia here. The role of the Apuseni Mts was recognized also in the speciation of the fish *Barbus* (Kotlík and Berrebi 2001). Species or lineages in the Apuseni Mts are often connected with the Southern Carpathians (the shared central haplotype of *C. maclachlani* is a good example, Fig. 11.1b).

The Timiş and Cerna rivers separate the Banat and the Serbian Carpathians from the Southern Carpathians. Babik et al. (2005) reveals an old endemic *COI* (mtDNA) lineage for *Lissotriton vulgaris* in this region. None of the aquatic insects discussed above were sampled here, but numerous endemic species are known. These mountains are often connected to the eastern massif of the Balkan Peninsula (Schmitt 2009).

The Southern Carpathians are bordered by the Prahova river in the east. The importance of this valley as a dispersal barrier is clearly shown by the range of many Southern Carpathian microendemics. For aquatic insects, haplotypes present only in this region were found in *D. romanicus*, both *P. occulta* species and

Table 11.1 Species endemic to major ranges of the Carpathians

		Apuseni Mts	Banat and Serbian Carpathians	Southern Carpathians	Eastern Carpathians	Western Carpathians
Oligochaeta	*Fridericia simeani*	X				
	Tatriella slovenica					X
	Trichondrillus tatricus					X
Isopoda	*Hyloniscus motasi*				X	
Orthoptera	*Chorthippus acroleucus*			X		
	Isophya harzi			X		
	Odontopodisma acuminata	X				
	Podismopsis transsylvanica			X		
	Uvarovitettix transsylvanicus			X		
	Zubovskia banatica			X		
Trichoptera	*Allogamus dacicus*			X		
	Allogamus lazeri					X
	Allogamus starmachi					X
	Allogamus tatricus					X
	Annitella chomiacensis				X	
	Drusus doehleri					X
	Hydropsyche sinuata		X			
	Potamophylax millenii			X		
	Psilopteryx curviclavatus	X				
	Rhyacophila carpathica			X		
	Rhyacophila cibinensis			X		
	Rhyacophila fagarashiensis			X		
	Rhyacophila kimminsiana			X		
	Rhyacophila motasi	X				
	Rhyacophila orghidani	X				
Plecoptera	*Leuctra transsylvanica*	X				
Heteroptera	*Acalypta carpathica*			X		
Coleoptera	*Carabus rothi alutensis*			X		
Thysanoptera	*Phloeothrips bacauensis*				X	
Diptera	*Idiocera paulsi*				X	
Lepidoptera	*Erebia manto traianus*			X		
	Erebia melas carpathicola				X	
	Erebia melas melas			X		
	Erebia melas runcensis	X				
	Erebia pharte romaniae			X		

(continued)

Table 11.1 (continued)

		Apuseni Mts	Banat and Serbian Carpathians	Southern Carpathians	Eastern Carpathians	Western Carpathians
Plants	*Aquilegia transsilvanica*			X		
	Astragallus pseudopurpureus				X	
	Carduus lobulatiformis			X		
	Centaurea carpathica				X	
	Daphne arbuscula					X
	Dianthis henteri			X		
	Draba dorneri			X		
	Draba simonkaiana			X		
	Erysimum witmanni transsilvanicum			X		
	Hieracium levitomentosum				X	
	Hieracium pojoritense				X	
	Lychnis nivalis				X	
	Poa molinerii glacialis			X		
	Poa nemoralis rehmanni				X	
	Poa tremula			X		
	Primula baumgarteniana			X		
	Primula leucophylla				X	
	Pulsatilla slavica					X
	Thlaspi dacicum banaticum			X		

After Beldie (1967), Botoşaneanu (1975), Csuzdi and Pop (2007), Kapusta (2009), Kis (1980), Mey and Botoşaneanu (1985), Mohan et al. (1993), Murányi (2007), Rákosy (1998), Starý and Ujvárosi (2005), Varga (1975, 2002)

A. compacta (Fig. 11.1a, c, d, e). Studies on other taxa also reveal endemic genetic lineages for e.g., butterflies (Schmitt et al. 2007) and fish (Sedivá et al. 2008). The Olt valley separates these mountains into a western and an eastern range. The make-up of genetic lineages of *A. compacta* indicate recent regression of populations into these regions. The valley forms the eastern distribution limit of *R. carpathica* populations. Signs of advanced lineage sorting are also present. The existence of distinct glacial refugia (one in the eastern and two in the western Southern Carpathians) was also shown for the butterfly *Erebia medusa* (Schmitt et al. 2007). The most important mountain in the Southern Carpathians regarding endemic species and lineages is the Bucegi. *Drusus romanicus* and both species of *P. occulta* have distinct lineages here (the location of the Bucegi and its endemic lineages are marked by arrows on Fig. 11.1).

The Eastern Carpathians are delimited by the Vistula river in the west and can be divided into a northern and southern range. The former is limited by the Rodnei Mts in the south and is rich in microendemics. Several haplotypes of *A. compacta* were recovered from the northern part. The Norway spruce (*Picea abies*) shows a major genetic change in this range: the northern and southern Eastern Carpathian populations have distinctly different mitochondrial minisatellite composition (Tollefsrud et al. 2008). The distribution of microendemics often shows connections between the Eastern and Southern Carpathians, but links between the Eastern Carpathians and the Apuseni Mts (like those in the case of *P. occulta* species B and *E. medusa*) are rare. Endemic haplotypes were found for *A. compacta, C. maclachlani,* and *D. discolor* in the Western Carpathians, suggesting the existence of glacial refugia there. A mitochondrial lineage of the smooth newt is endemic to the Western Carpathians and the northern Eastern Carparhians, showing the frequent connections observed between these regions (Babik et al. 2005).

Pre-Pleistocene geological processes are responsible for the formation of several taxa (e.g., Csuzdi and Pop 2007). Many highly divergent genetic lineages were probably also formed prior to the Pleistocene. The survival of these ancient entities and the formation of younger lineages was possibly mediated by climate cycling during the Pleistocene. The long-term existence of suitable habitats for various organisms during several climate cycles is probably related to the high topographical diversity of the Carpathians, creating large numbers of microhabitats, which are climatically independent from the surrounding areas. For example, deep valleys with running waters and relatively stable microclimate can be found in all mountains that also exhibit endemic taxa or lineages. Strong climatic variability in this area might allow short-distance dispersal to suitable habitats. In contrast to the Pyrenees or the Alps these valleys were only partially covered by ice even during the coldest periods of the last glaciation (Reuther et al. 2007).

All organisms that survived glaciations in the Carpathians or in areas nearby had to be cold tolerant. The accessibility of permanent water sources probably played a more important role for their survival than low temperatures. Continental species, such as the adder *Vipera berus* or the woodland ringlet are currently present in Central Asia, South Siberia, and Southern Ural, where winter temperatures are comparable with those in Europe during the LGM. The distribution of these species is limited by aridity rather than low temperatures, so their survival was possible close to more humid mountains, like the Carpathians (Schmitt 2007).

Arctic–alpine species were even able to expand their ranges under a colder climate (Schmitt and Hewitt 2004), especially during the milder periods of the last glaciation. These species usually had a larger continuous distribution during the cold periods. High-altitude or cold areas (e.g., particularly cold valleys and basins) of the Carpathians and other Central European mountains represent interglacial refugia for these species during a warmer climate.

Some terrestrial mountain species were able to survive the glaciations in ice-free areas among glaciers (nunataks), in the border areas of mountains (peripheral refugia), and outside the mountains and beyond ice sheets in lowland refugia (recently reviewed and referenced in Holderegger and Thiel-Egenter 2009; Schmitt et al. 2010). As the glaciers were not extensive in the Carpathians, the limiting factor for the survival of terrestrial mountain organisms was probably habitat humidity and availability of water, as in the case of continental species.

Flowing water environments are stable over long periods of time, buffering the effects of atmospheric temperature changes. This facilitates the long-term survival of numerous mountain aquatic species under changing climate conditions (Malicky 1983, 2000). When the climate cools and glaciers advance, aquatic species descend to lower altitude habitats nearby. In times of warming the stream sections providing ecologically suitable conditions (e.g., high oxygen concentrations, low amounts of dissolved organic matter, etc.) can be found at higher elevations, and populations follow them with relatively short vertical range displacement. The peculiar characteristics of glaciations in the Carpathians may be responsible for the large number of winged aquatic endemics. As mentioned above, glaciers were not extensive in the Carpathians. There was a considerable reduction in precipitation especially during the LGM, as water was trapped in extensive icesheets of the Northern Hemisphere. This resulted in generally drier conditions around the mountains. Consequently, glaciers were less expansive, reaching only e.g., 1,050 m a.s.l. in the north-facing Pietrele Valley of the Retezat Mts during maximum advance (western part of the Southern Carpathians – Reuther et al. 2007). Meltwater is always present below the glaciers at least during the summers, providing suitable habitats for stream-adapted species. As the glaciers never extended to very low elevations in the Carpathians, the lower reaches of the valleys provided sufficiently long inclines to support permanently flowing streams that could sustain significant aquatic communities. Communities were probably not "pushed" out to the lowlands, where changed ecological conditions related to lower water velocity could result in their disappearence. As species possibly remained within the valley systems, the chance of secondary contact among lineages previously isolated at high altitudes was reduced.

11.5 Conclusions

Our knowledge of scale and patterns of genetic diversity in the Carpathians is increasing. This first synthesis shows strong similarities among geographic structures of the molecular diversity and the distribution patterns of microendemic taxa. The Carpathians certainly served as refugia for numerous species and lineages during the past climatic oscillations, which may account for their high level of diversity. Genetic population structure found in several aquatic insects, but also in vertebrates and other terrestrial species are consistent with the existence of microrefugia in the Carpathians.

There is a need for more detailed molecular studies to clarify and understand the role of these mountains in the formation and survival of numerous taxa and lineages, as the importance of genetic diversity in the conservation of species is increasingly recognized (see e.g., Schmitt 2007). Areas with high genetic diversity play a central role in the preservation of significant proportions of a species' diversity and its evolutionary potential (Taberlet and Cheddadi 2002). Understanding the genetic diversity patterns in the Carpathians is essential for efficient conservation management of these relatively pristine regions, where we may be able to minimize the impacts of recent, ongoing and particularly rapid development of Central-East European economies.

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Part III
Biodiversity in Madagascar

Chapter 12

Conservation in a Biodiversity Hotspot: Insights from Cultural and Community Perspectives in Madagascar

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Abstract High levels of endemic biodiversity, habitat loss and degradation have made Madagascar one of the planet's biodiversity hotspots. While protected areas are a sensible approach to preserving valuable ecosystems and their services, they are a conservation concept that often struggle to fully consider the local social and cultural characteristics of the areas where they are established. Protected areas are frequently inhabited by local people who directly depend on natural resources for their livelihoods, and whose beliefs and customary tenure systems have often become closely intertwined with the land over long periods. The conservation movement in Madagascar has made considerable efforts to develop viable models for conservation incorporating local communities, for example through community-based natural resource management models. However, a closer examination of the implementation of these models illustrates a cultural clash between the different ways of life, ambitions and world views of local recipients and external implementers.

Increased consideration of local people's values and cultural practices combined with integrative scientific understandings of conservation from both natural and

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social science could lead to an improvement of conservation policies and implementation in terms of both conservation effectiveness and socio-economic equity. We conclude by presenting suggestions for a basis from which actions can be taken to improve the coherence between forest conservation policies and culture. More participatory policy development and implementation processes, improved dialogue, recognition of customary tenure systems, and more comprehensive and timely livelihood solutions should lead to more balanced forest conservation strategies to ensure that ecosystem services can be sustainably provided to both the local and global community.

Abbreviations

ANGAP	Association Nationale pour la Gestion des Aires Protégées
CBNRM	Community-Based Natural Resource Management
COBA	Communauté de Base (Basic community for local forest management)
GCF	Gestion Contractualisée des Forêts (Contracted Forest Management)
GELOSE	Gestion Locale Sécurisée (Secured Local Management)
HPI-1	Human Poverty Index
ICDP	Integrated Conservation and Development Projects
IIED	International Institute for Environment and Development
IUCN	International Union for the Conservation of Nature
Mha	Million hectares
MNP	Madagascar National Parks (former ANGAP)
NEAP	National Environmental Action Plan
NGO	Non-Governmental Organisation
NPA	New Protected Areas
PPNT	Propriété Privée Non Titrée (Untitled private land recognised as legal under 2006 land reform laws)
SAGE	Service d'Appui à la Gestion de l'Environnement (Environmental Management Service)
SFR	Sécurité Foncier Relative (Relative Tenure Security, under the GELOSE legislation)

12.1 Introduction

Conservation policies are designed with the primary objective of preserving biodiversity and ecosystem services for human well-being. Conservation organisations and research agencies have played an important role in both the development and implementation of community forestry policies and in the establishment of new conceptual designs of protected areas that highlight the human dimension in conservation. However, there is no shortage of social critiques of the ethics, conception, design and implementation of forest conservation in Madagascar (some pertinent are: Corson 2008; Harper 2008; Henkels 2001; Horning 2004, 2005, 2006; Kaufmann 2006; Keller 2008, 2009; Muttenzer 2006; Pollini 2007; Simsik 2004; Walker 2001). While the studies behind these criticisms are often based on particular localities, organisations or processes, they also provide insights relevant across Madagascar's forest conservation policies. It is evident that anthropological perspectives on the human dimensions of forest conservation policy in Madagascar has only partially influenced the policy development process, as has been observed in other developing world regions where conservation has been studied (Peterson et al. 2010). Participation as it is promoted for a better involvement of people living in or nearby protected areas often remains more like a slogan than an effectively implemented approach, with placatory and consultative forms of participation typically dominating, rather than the more empowering and decentralising forms which may be aspired to.

In this chapter we briefly introduce the context of conservation in Madagascar, which classifies the country as a biodiversity hotspot; we then complement this with some insights from social and cultural perspectives with the aim of providing a more balanced portrayal of the conservation arena on the island. Next we present the underlying ideas of nature conservation, showing how they are embedded within the ideology of the developed world; this is followed by an overview of conservation activities in Madagascar and analysis of the challenges of applying the concepts of protected areas and community-based natural resource management. The article closes with a discussion on the role of scientists in forming part of innovative conservation partnerships with practitioners and communities and concludes with recommendations to let local identities and aspirations move into the centre of conservation initiatives.

12.2 Ecological, Socio-economic and Cultural Insights from Madagascar

12.2.1 Biodiversity Status and Developments

The definition of biodiversity hotspots is based on two phenomena: on the biodiversity side, hotspots are areas with exceptional plant species richness and concentrations of endemic species; on the socio-economic side, hotspots become hotspots because they have lost more than 70% of their original primary vegetation (Myers et al. 2000). From the biodiversity point of view, Madagascar certainly qualifies as one of the top biodiversity hotspots on earth.

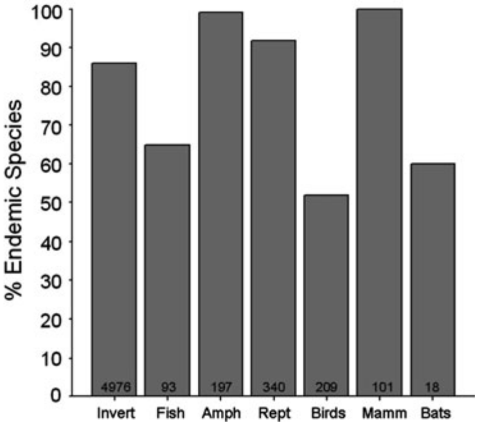

Fig. 12.1 Degree of terrestrial animal endemism in Madagascar. *Numbers* indicate species numbers as of 2005. The number of species described has increased in all taxa since publication of these data in 2005 (from Goodman and Benstead 2005)

Madagascar's plant species richness is exceptional (Barthlott et al. 1996) and more than 90% of its 13,000+ plant species are endemic (Phillipson et al. 2006). Faunal diversity parallels plant species diversity. As of 2005, vertebrate taxa show between c. 50 and 100% of endemism (Fig. 12.1). Invertebrates are far from being described to the extent that would allow any definite statement but the degree of endemism is expected to be at least as high as in vertebrates (Goodman and Benstead 2005).

Madagascar's biota evolved in isolation until the arrival of humans approximately 2,300 years ago. This arrival was followed by a rapid loss of native large vertebrates (Burney et al. 2004), for which humans were likely to have been largely responsible. Original forest cover is difficult to estimate (Lowry II et al. 1997). In 1953, 27% (or 160,000 km^2) of the island was still covered with forest. This was reduced to 17% (or 99,000 km^2) in 2000 (Moat and Smith 2007). Apart from the simple loss of forest cover, the remaining forests are highly fragmented with more than 45% of forest existing in patches of <500 km^2, and over 80% of forest area was <1 km from an edge in the year 2000 (Harper et al. 2007).

The concepts of "Biodiversity hotspots" and "Wilderness areas" have been developed as a means to draw attention to the integrated phenomena of evolution and human activities and thus to reconcile human needs and the conservation of unique biota (Mittermeier et al. 2004; Myers et al. 2000). However, in Madagascar subsequent approaches focussed on the distribution of biota (Goodman and Benstead 2003), the possible evolution of centres of endemism (Wilmé et al. 2006) and the design of protected areas to maximize taxonomic coverage by protected areas (Andreone et al. 2008; Kremen et al. 2008) in a landscape affected by climatic change (Hannah et al. 2008). Yet, it had been evident early on that biotic conservation is at risk without consideration of socio-economic issues (Ganzhorn and Sorg 1996; Ganzhorn et al. 2001; Jolly et al. 1984; Kremen et al. 1999; Sayer 2009).

12.2.2 Socio-economic Status and Developments

12.2.2.1 Country Background

In contrast to its natural richness, the socio-economic situation, especially in rural areas of Madagascar, is poor. With a Human Poverty Index (HPI-1) value of 36.1% in 2009 (UNDP 2009), Madagascar is the 23rd poorest country among the 135 countries for which the index has been calculated[1]; the standard of living can be considered very low. In many remote areas tarred roads and bridges, electricity and access to sanitation facilities is quasi absent, while much of the existent infrastructure, mainly established during colonial times, is rarely properly maintained. Under the auspices of the Millennium Development Goals, the government and the private sector have invested in the establishment of a countrywide communication network providing mobile telephone connections and internet access to many new areas (UNDP 2006). Education programmes have also been strengthened; however, adult illiteracy rates remain at about 30% (UNDP 2009). Income and livelihood security are unstable and even negatively affected by high inflation. The majority of rural Malagasy derive their livelihoods from subsistence farming and for those who live in or near the remaining forests, through the collection/extraction of natural resources in the forests. Forest resources provide Malagasy people with products from housing material to food, and medicine to fuel wood, which are all essential for their livelihoods. Typically those people, who are the most dependent on forest resources and who have the least available alternatives, are those living in very remote areas with limited access to markets and few employment opportunities (PROFOR 2008). According to an investigation conducted by IIED and Foniala (2008) on the relationship between poverty and forest dependency, forest products contributed significantly to rural incomes (26% in humid forests and even 30% in dry forests) forming a major part of farmers' subsistence incomes (35–80%). The island's human population (currently at about 20.5 million) is growing at 2.7% annually (UNPF 2008) and contributes to a further increased use of forest products. Sixty-one per cent of the Malagasy people live outside urban areas and rely on natural resources. This reliance often causes disturbances in natural ecosystems (Irwin et al. 2010).

12.2.2.2 Evidence on Land Clearance Due to Anthropogenic Threats

Meeting human livelihood needs is among the most significant drivers for deforestation in Madagascar. According to literature on deforestation (e.g. Casse et al. 2004; Elmqvist et al. 2007; Sussman et al. 1994) four categories appear on a list of

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[1] The HPI-1 measures severe deprivation in health by the proportion of people who are not expected to survive to age 40. Education is measured by the adult illiteracy rate.

main anthropogenic threats: (a) cropland expansion, (b) fuel wood collection/charcoal production, (c) timber exploitation, (d) expansion of grazing lands (pasture).

As in many tropical countries, slash-and-burn agriculture is the dominant agricultural practice in forested areas and frontiers (Styger et al. 2007); this shifting cultivation system may or may not involve periods of fallow and reuse of fields. While this cultivation method is considered by some authors to have been sustainable when human population densities were lower (Erdmann 2003), today it is considered to be the primary threat to Madagascar's forests leading to substantial areas of tropical forest being cleared and subsequent soil erosion. The resulting soil fertility decrease in combination with limited active management of water resources pushes the people to further deforest new land (Durbin et al. 2003). In the northeast of Madagascar, for example, a great part of households are believed to constitute 50–65% of their annual consumption from slash-and-burn cultivation (or *tavy*,[2] *tetik ala, hatsake, tevy ala* as it is called in different regions of Madagascar) (Ghimire 1994), which leads to an average surface clearance of 2 ha/p.a. per family (Kistler and Spack 2003). With the practice of *tavy* considered incompatible with conservation, forestry and conservation legislation mainly aiming at the control of *tavy* emerged (Evers et al. 2006; Ghimire 1994; Pollini 2007). Thereby primarily climatic, topographical, economic, and livelihood-related rationales provide the basis of knowledge used to control impacts of *tavy* practices. However, the threats vary significantly from place to place, and local people often have their own pre-existing local traditional customs, which regulate natural resource exploitation and land conversion such as, for example designated areas in which it is prohibited to use *tavy* (Kistler and Spack 2003).

12.2.3 Customary Land Use Systems Formed by Socio-culture

As slash-and-burn agriculture or *tavy* is a common practice to cultivate tropical soils in Madagascar, it is also locally considered as a legitimate means to assert ownership of land. There have been a number of studies on the complexities of land tenure systems on the island (e.g. Evers et al. 2006; McConnell 2002; Muttenzer 2006, 2010; Pollini 2007; Sandron 2008) especially dealing with the many discrepancies between national legislation and local customary rights that hinder a consistent regulation throughout the country and may result in land tenure insecurity for rural people. While land tenure is officially regulated through a national titling system, which is partly a product of French Civil Law, in practice in most cases local customs govern the allocation of land in rural areas. A lot of criticism has been made of the efficacy of the centralised land registry system,

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[2] In the following *tavy* is used as substitute for the various Malagasy terms of slash-and-burn agriculture.

because it lacks on the one hand implementation due to difficult, costly and time-consuming procedures to register a land title and is on the other hand often not coherent with locally legitimised forms of land tenure, for example when land is forested or located within protected areas (Kull 2002; Muttenzer 2010). Whereas local customs mostly lack documentation and are mainly derived from local honour agreements (Evers et al. 2006) that prove to be barely capable of being conceptualised and integrated into common law (with few exceptions in some regions, where "small papers" are distributed containing basic information such as the identity of the title holder and the nature of the land title the holder is (locally) approved to own (Teyssier 2010)). Such honour agreements on land use are influenced by socio-cultural aspects such as (1) kinship (ancestors and descendants) and their solidarity (*fihavanana* or *filongoa*) with each other; (2) social codes (*dina*); (3) taboos (*fady*); (4) traditional leaders and (5) the belief in supernatural and ancestral spirits, briefly introduced in the following.

The Malagasy expression *Fihavanana* encompasses the native concept of kinship, friendship, goodwill between beings, both physical and spiritual. The literal translation is difficult to capture, as the Malagasy culture applies the concept in unique ways. Its origin is havana, meaning kin. It comes from the belief that we are all one blood entailing the idea that the way we treat others will eventually be reflected back to us and that we, therefore, should be proactive about goodwill for the good of the world. *Fihavanana* is not limited to the present but can also be applied to our relationship with the spiritual world. *Fihavanana* or kinship is the intimate relation between the members of a family, extended to a deeper friendship between people of the same community and lastly with people of the same land. In Malagasy, proverb and ritual discourse, there is often a deliberate reinforcement of the importance of this kinship.

Dina are traditional (in many cases oral) codes of conduct or pacts that regulate relationships within and between communities. Through the application of *dina* as customary law community behaviour and access to resources is guided and controlled (Rakotoson and Tanner 2006). It is also an informal legal mechanism that stipulates fines (called the *vono dina*) in case of rule breaking. In general, in order to establish a legitimate *dina* the majority of the general assembly of village inhabitants (the *fokonolona*) needs to agree on its terms. There are several forms of *dina* concerning different areas of life such as trying and punishing crime, to tie traditional customs with modern law, to interpret contractual relations and to maintain security (Henkels 2001).

In Malagasy culture taboos called *fady* (or *faly*) regulate life in the community and establish norms for what is prohibited or allowed. Some *fady* refer to places; others can refer to permissible or forbidden times for agricultural activities or cultural events, and may also relate to behaviour and language deemed acceptable for use towards elders, etc. (Jones et al. 2008; Stifel et al. 2009). "To respect *fady* is to respect world order. *Ota fady*, to break *fady*, is dangerous. You will have *tsiny* [blame] and most probably be hit by *tody*, the retaliating force (. . .). . . . Taboo-breakers are a disgrace to their home and community, as they bring the whole community out of the normal status and into a dangerous position." (Dahl 1993:

79). People in Madagascar live and think *fady* rather than considering taboos as formulated written rules, in other words they are held within their consciousness and thus intrinsically govern their behaviour (Lambek 1992).

Traditional leaders ensure the provision of justice in local villages, foster solidarity among the members of the clan, village or commune and assure the transmission of traditions and customs. People are required to accept their authority as long as they live in the same village (Henkels 2001). The influence of traditional leaders is still significant in many rural places in Madagascar, although existing in distinct forms within individual ethnic groups. Some are organised by independent monarchies (kings), others by the traditional priests (*mpisoro*) or lineage elders. For example to the Sakalava ethnic group the king (*ampanjaka*) represents the link between spiritual heaven (god) and material earth (people) and thus his will is respected for this reason. Having this function the king is closely connected to royal ancestors who are the most powerful in society (Feeley-Harnik 1978). Notables (in some regions called *Ndaty be* or *Olo be*), who are the village elders, share their knowledge and views with the leader to support his decision-making, while these procedures follow strict rules be they for ceremonial or more everyday processes.

Belief in supernatural and ancestral spirits as well as other mythical beings is an important part of the cultural attachment to the land for many rural Malagasy.[3] Although the specificities vary across the island, place-based spirits include ancestral spirits (*lonake, raza*) which exist around burial sites; the resurrected ghosts of the dead (*lolo vokatse*/*lolo mifoha*); malevolent spirits and healing genies (*kokolampo, lolo mpamosavy*) associated with treatment by traditional healers (*ombiasy*); spirits of visitation from ancestors (*angatse*); feared human-like forest dwelling beings (*kotoki, kalanoro, vazimba*); and wild animal-like creatures (e.g. *tratrake*). These spirits and beings are central to traditional Malagasy religions and they are often place-based, meaning that sites may come to be considered sacred, feared, and cursed or dangerous. While understanding such cultural characteristics in isolation is neither desirable, nor possible (Keller 2009), it can be said that they comprise a tenet of the customary conception of land tenure. The existence of such spirits in a given area is among the elements leading to people becoming owners of the land (*tompotany*) when ones' ancestors pass from living spirits (*fanahy*) to become deceased ancestral spirits (*angatse*) and are buried on the land. These cultural aspects exert a direct influence on customary land tenure that is summarised in Table 12.1.

By considering the multifaceted nature of socio-cultural aspects of Malagasy society that play a role in customary land use systems, it becomes apparent that traditional customs vary from fixed norms defined in law through to landmarks and guiding principles which provide the basis of social identities. They also vary from place to place and are mostly not predicated on an environmentalist rationale,

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[3] There is an extensive literature discussing Malagasy spiritual beliefs from which this summary is drawn: Astuti 1995, 1997; Benolo 1992, 1996a, b; Decary 1933; Faublée 1954; Fee 2001; De Flacourt 1995; Graeber 2007; Heurtebize 1997; Jaovelo-Dzao 1996; Rudd 1960; Vig 2001.

Table 12.1 Examples of socio-cultural aspects influencing honour agreements in rural areas in Madagascar

Kinship (ancestors and descendants) and their solidarity (*fihavanana*) with each other	Land ownership is influenced by kinship networks and based on conventions and practices of solidarity between relatives including non-related but closely connected persons and families. Traditionally, it is believed that ancestors prohibit the sale of land, also because tombs are built on the land of the ancestors and thus constitute family authenticity (Evers et al. 2006). A kin's successful growth depends on the provision of land to descendants, since land means life not only for subsistence purpose but rather for enabling the process of continuation and growth through offspring (Keller 2009). Practices of land inheritance between parents and their children are a tangible example (Evers et al. 2006). Hence, the possession of land is directly connected to growth and well-being of a kin.
Social code (*dina*)	*Dina* regulate the use of resources of people's territories in and around villages. Local actions are measured by means of the *dina* in order to guarantee a fair use. However, the application of *dina* is sometimes difficult, since every *fokontany*[a] and sometimes even village has its own interpretations and therefore, access regulations can differ from place to place. For example, a person who exploits the forest outside his own village boundaries may not feel obliged to comply with the rules of the other village (Fritz-Vietta et al. 2009).
Taboos (*fady*/*faly*)	Also taboos regulate the use of natural resources through rules of action towards plants, animals, areas, etc. For example, within fallow lands particular trees or a group of trees are protected by taboos (*fady*), which residents explain as result from bad luck that befell someone who once tried to clear the land (McConnell 2002). In many ethnic groups whole territories are called taboo (*tany fady*) where no use is allowed, variously due to the presence of ancestral tombs or the presence of supernatural sprits/beings or the areas function as a healing area.
Traditional leader	In many cases, local leaders (*ampanjaka*) hold the control over all the land in their sphere of influence (Müller and Evers 2007). If migrants wish to claim new land rights, the leaders tackle them with deep questions about matters such as their background, the original place of their ancestors (Evers 2009). In the case of conflicts traditional leaders have a responsibility for conflict resolution, which is to be respected in cases of land rights as it is for livestock theft and other transgressions of cultural norms which may enter the customary court system.
Beliefs in supernatural spirits/beings	The existence of various supernatural spirits and mythical beings/creatures plays an important role in regulating access to given area in the landscape as well as the use of resources contained thereon. The reason for particular patterns of behaviour around place based spirits may be because of the existence of an associated *fady,* fear of being attacked, poisoned or cursed, or simply due to respect of the ancestors and obligation to maintain the cleanliness and integrity of their burial sites.

[a] *Fokontany* is Madagascar's smallest state recognised administrative unit, usually consisting of several villages and up to a couple of thousand people.

although they are often coincidentally beneficial to nature conservation but can also exist to its detriment (such as the requirement to use particular species for coffins or the prohibition of touching invasive species on sacred grounds). It can be said that the designation of protected areas adds another new form of "land use system" to the nuanced relationship which local people have with the land and its natural resources upon which they rely.

12.3 Conservation Policy in Madagascar

12.3.1 Nature Conservation: An Idea Born in Industrialised Countries

In contrast to what we have described already of the Malagasy rural social order, it could be argued that societies of the developed world became relatively detached from their natural environment both physically and spiritually due to developments such as the advent of industrial agriculture, long-distance trade, as well as trends towards increased occupational specialisation, and urbanisation. Increasing secularism, humanism, and materialist tendencies as seen in Western society have changed our ways of understanding and engaging with the interrelatedness of nature and culture. Nature conservation emerged from this context and gained particular recognition when the tremendous loss of biodiversity became known, because environmental studies discovered disastrous impacts of for instance the extensive use of chemicals in agriculture (e.g. Rachel Carson's book "The Silent Spring" (1962)) and the increasing demand of natural resources due to the ever faster growing technological markets. Kaufmann (2006) embraces this fact revealingly as an "enlightened environmentalism – with roots in modern over-consumption pushing the earth to its limits" (Kaufmann 2006: 181).

Most recently, proponents of conservation developed the concept of functions and services to ecosystems such as watershed protection, medicinal plants, pollination or a 'sense of place' at large that might be seen differently by local people than tourists but ultimately leads to the preservation of a pristine ecosystem (Carpenter et al. 2009; de Groot et al. 2002). Some of these functions and services can be fulfilled by anthropogenically modified systems, others cannot. The argument in favour of nature preservation is now formulated that these services and functions have to be maintained in order to arrive at sustainable forms of land use. Despite there being a remarkable tendency from pure protection towards more integrative conservation and development models in recent decades, the underlying ideology arguably remains in opposition to the local cultural identities and aspirations of people in non-western countries, and this is often reflected in the externally led designation processes and the configurations of protected areas in Madagascar.

12.3.2 Designation of Protected Areas in Madagascar

Conservation policy's first mission is the preservation of biological diversity and maintenance of ecological processes. In the case of Madagascar as Goodman and Benstead (2003) acknowledge in their volume "The Natural History of Madagascar", the number of biologists has increased in the past decades almost exponentially and with it the amount of knowledge on the island's biological and ecological phenomena. These investigations contributed considerably to the progress of conservation initiatives in Madagascar acting under the realm of "Madagascar: a biodiversity hotspot" with the aim of "wilderness protection" which led to the designation of numerous protected areas (Kremen et al. 1999; Wright 1994). Priority conservation areas have been principally concentrated on sites with high levels of biodiversity importance, usually indicated by localised endemism and/or high levels of extinction risk and threat of habitat clearance (ANGAP 2001). The areas which have during the twentieth century become protected areas were in many cases relatively unfavourable to permanent human settlement and intensive sedentary agriculture due to factors such as accessibility, topography, soil fertility and irrigability. As a consequence these areas often had relatively low human population densities meaning that they could be feasibly conserved using one of the three strictest IUCN protected area categories (I, II, IV) without necessitating much physical displacement of people from these areas, indeed most of the protected areas created before 2003 fit into one of these types (Table 12.2).

In 2003 the then president of Madagascar, Marc Ravalomanana, was convinced by part of the international conservation lobby to adopt a policy where his government would triple the area of Madagascar's protected areas to attain IUCN targets of 10% of Malagasy territory covered by protected areas within 5 years (Corson 2008); this policy became known as the "Durban Vision", at the World Parks Congress in Durban. In the 6 years since the Durban Vision, the surface under protection has expanded from 1.76 Mha to 6.03 Mha (Nicoll 2011) now covering 10.2% of Madagascar's land area. However, it is noteworthy that with its commitment to triple the coverage of protected areas the Malagasy government was focused on meeting donors' aspirations (Horning 2009; Simsik 2004). As a consequence the government has to manoeuvre within relatively strict boundaries imposed by the donors, threatening Malagasy governmental autonomy comparable with conditions of the agreement on the National Environmental Action Plan (NEAP[4]). The NEAP was initiated in the early 1990s by the government, based on the Malagasy Environmental Charter adopted in 1990 that in turn had been

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[4] NEAPs have been applied in many countries; in the foreground of the implementation of a NEAP is the commitment of the government to design development programmes and projects as environment-friendly as possible (Kamps 2000) and to build political support for environmental goals (Brinkerhoff 1996) as is in the case of Madagascar, also reflected in the Madagascar Action Plan (Madagascar Government 2005).

Table 12.2 Categories of protected areas in Madagascar

IUCN category	IUCN management objectives	Madagascar's application of IUCN management categories (Madagascar government 2008)
I	Strict Nature Reserve: Managed mainly for science. Wilderness Area: Managed mainly for wilderness values.	Réserve Naturelle Intégrale (RNI) *TAHIRIN-JAVABOAARY* Integral Nature Reserve
II	National Park: Managed mainly for ecosystem protection and recreation.	Parc National (PN) & Parc Naturel (PNAT) *VALAN-JAVABOAARY* National Park & Natural Park
III	Natural Monument: Managed mainly for conservation of specific natural features.	Monument Naturel (MONAT) *TAHIRIM-BAKOKA VOAJANAHARY* Natural Monument
IV	Habitat/Species Management Area: managed mainly for conservation through management intervention.	Réserve Spéciale (RS) *TAHIRIN-JAVABOAARY* Special Reserve
V	Protected Landscape/Seascape: managed mainly for landscape/seascape conservation and recreation.	Paysage Harmonieux Protégé (PHP) *TONTOLO MIRINDRA VOAARO* Protected Harmonious Landscape
VI	Managed Resource Protected Area: managed mainly for the sustainable use of natural ecosystems.	Réserve de Ressources Naturelles (RRN) *TAHIRIN-KARENA VOAJANAHARY* Natural Resource Reserve

strongly influenced by the United Nations (Henkels 2001). For its adoption the government has been relying on the assistance of international lenders/donors then lead by the World Bank (Brinkerhoff 1996; Gezon 1997; Kamps 2000; Madagascar Government 2005).

In order to meet the ambitions of the Durban Vision it was necessary to establish dozens of New Protected Areas (NPAs) across parts of Madagascar that often comprise significant numbers of human settlements within their boundaries, and whose residents often had high levels of dependence on the use of timber, bushmeat and other forest resources as well as the clearance of the forest for subsistence farming. Therefore, these NPAs typically fell into IUCN Categories III, V and VI (Table 12.2), which are characterised by a less strict protection status than category I, II and IV to allow for sustainable resource use in these areas. Legislation for these new types of protected areas which was introduced following the Durban declaration allows for multiple use zoning and various forms of collaborative management. They are often based on federations of local community associations (V.O.I., COBA or CLB[5]) who are responsible for managing forests which have been transferred to them using community forestry contracts under GELOSE and GCF acts (as described in the next section). Since the Durban Vision, the integration of

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[5] V.O.I.: Vondron'Olona Ifotony; COBA: Communauté de Base; CLB: Communauté Locale de Base (which are all local institutions).

new protected area categories into the Malagasy legal system has meant that the social dimensions of conservation policy development are becoming increasingly important in determining conservation success and ensuring local people do not suffer as a consequence of conservation interventions.

12.3.3 Community-Based Natural Resource Management in the Vicinity of Protected Areas

At the time the NEAP was initially rolled out, an array of Integrated Conservation and Development Projects (ICDPs) were implemented in Madagascar (including flagship ICDPs at Ranomafana, Ankarana, Andohahela, Masoala, Zahamena and Beza Mahafaly) (e.g. Hanson 2007). The ICDP concept aimed to provide sustainable livelihoods, education and health intervention on the periphery of national parks. The fundamental idea was to preserve ecosystems through the designation of core conservation zones as new National Parks or Special Reserves, or redesignating former Integral Nature Reserves. Areas around these core zones were reserved for community-based management, and various agricultural, health, education and livelihood diversification projects, in order to address both ecological and socio-economic needs (Kremen et al. 1999). Subsequently, policy reforms in forestry and land tenure legislation opened up the possibility of delegating management responsibility for natural resources to local user associations, through community-based natural resource management (CBNRM) contracts. The 1996 policy, known as Gestion Locale Sécurisée (GELOSE) meaning Secured Local Management, allowed contracted time-bound transfers of management activities of natural resources to local communities. In implementation, GELOSE was applied mainly to forests, although some marine and freshwater fishery sites have also been transferred (Antona et al. 2002). In 2001 a simplified version of the policy was enacted specifically intended for forests, known as Gestion Contractualisée des Forêts (GCF) meaning Contracted Forest Management, removed some of the administratively cumbersome aspects of GELOSE such as using environmental mediators in the development of the contracts, involving local communal administrations as signatories, and providing the possibility of relative tenure security (SFR – Sécurisation Foncière Relative) at the level of village lands (Kull 2002; Raik and Decker 2007).

Despite huge investments and considerable effort by international conservation organisations, in Madagascar these projects proved to remain relatively ineffective over the years (Kull 2002; Sayer 2009; Wells and McShane 2004) as has been the case in other countries (Leach et al. 1999; Wainwright and Wehrmeyer 1998). In spite of the recognition of socio-economic constraints inevitably resulting from the designation of protected areas and the attempt to integrate alternative activities into these schemes, the main challenges remain largely unsolved. These being (a) the provision of adequate livelihood alternatives to forest clearance/use before the imposition of new restrictions, and (b) the incompatibility between Western and Malagasy belief and land tenure systems and ambitions. Some examples of GELOSE and GCF implementation reveal this "culture clash" manifestly. As the evaluation report of transferred areas in the Mananara-Nord Biosphere Reserve stated, the primary goal of GCF is to establish a buffer (or green belt) around the national park in order to reduce pressure on the park and also to put people in charge of the management of the buffer zone (ANGAP-UE/IC 2007). The formal criteria of the management transfer to local communities are listed in Table 12.3 (following Pollini and Lassoie 2011), when these are considered in light of local socio-cultural characteristics described in Sect. 12.2.3 as well as accounting for the high profile position of conservation organisations reveals a number of issues (1) the discrepancy between intention and actual impact, (2) the power, profile, and dominant narratives of conservation organisations, and (3) the incompatibility of socio-cultural features and nature conservation as often defined by the international community.

Table 12.3 Community-Based Natural Resource Management (CBNRM) principles in contrast with socio-cultural aspects

Principles of CBNRM in Madagascar	Controversy/Incompatibility with local socio-cultural aspects (examples) and the remaining high profile of conservation organisations in the process
1. Contract between two (for GCF) or three parties (for GELOSE); between the forest administration and a local association (forest user group), and the local commune for the case of GELOSE	Where *fihavanana* acts as a significant force regulating the social order, a contract between local associations and the forest ministry may potentially fail in conflict situations in which people may behave according to their social affiliation, rather than in terms of delivery of the laws or rules of the contract. This is exemplified by the following proverb: "*Aleo very tsikalakalam-karena toy izay very tsikalakalam-pihavanana*" (Better to lose some material wealth than losing the relationship with kin or friends) (Rafolisy 2008). The make-up of the contract strongly bears the hallmarks of conservation organisations including management plans etc. that are difficult to understand for most rural people (Pollini and Lassoie 2011). As a consequence there is a reliance on oral commitments, between representatives of NGOs and the community, which often vary significantly from the substance of the written contracts (Hockley and Andriamarovololona 2007).
2. Creation of new institutions – local associations (abbreviated V.O.I. or in particular: COBA for GCF and CLB for GELOSE)	Local social structures are strongly influenced by family, lineage, clan and descent status (noble, free, former slave) and thus may influence the membership and structure of the newly established association; access for

(continued)

Table 12.3 (continued)

Principles of CBNRM in Madagascar	Controversy/Incompatibility with local socio-cultural aspects (examples) and the remaining high profile of conservation organisations in the process
	people of marginal groups can be more difficult (Bertrand 1999). Through the establishment of new associations specifically designed for the management transfer further social structures are added to traditional ones adding to complexity (Pollini and Lassoie 2011) and potentially reinforcing or subverting power dynamics, and ability to access resources.
3. Establishment of community rules (new *dina*)	While new *dina* are designed to fit the requirements of local management of natural resources, their legitimacy varies, since they are (1) created on the initiative of outsiders and (2) required to conform to state defined constitutional, legislative and regulatory dispositions, therefore, allowing relatively little room for negotiations as to their substance. Furthermore, the contents of GCF/GELOSE type *dina* need to be formally approved by the mayor, which may disempower the recognised clan leaders from their traditional role (Henkels 2001; Kull 2002). Furthermore, Evers and colleagues highlight that new rules "forced the local population to view surrounding forest in a different way" (Evers et al. 2006: 6), exploitation is strictly regulated and *tavy* is completely banned contradicting cultural habits of a number of Malagasy ethnic groups (Muttenzer 2010).
4. Existence of an environmental mediator: A specialised person who is in charge with consulting and supporting GELOSE contract negotiation.	In many cases the mediator is not a local person and is hired from a state-certified pool of specially-trained professionals (Kull 2002) and is often a representative of a conservation unit as it is the case e.g. in Mananara-Nord Biosphere Reserve, where Madagascar National Parks (ANGAP-UE/IC 2007) or in Sahamalaza Biosphere Reserve where SAGE (environmental management service) (ANGAP and MEEFT 2008) assume this role with efforts to convince people and raise awareness as it is their task in protected area management rather than performing their assignment as independent mediator (Fritz-Vietta et al. 2009).

(continued)

Table 12.3 (continued)

Principles of CBNRM in Madagascar	Controversy/Incompatibility with local socio-cultural aspects (examples) and the remaining high profile of conservation organisations in the process
5. Specifically for GELOSE – recognition of relative land tenure security (SFR)	The possibility which GELOSE established to recognise community level tenure security does not differentiate between communal forests, *de facto* private lands (in use, actively reserved for future use or in fallow). Furthermore, in most areas where GELOSE or GCF contracts have been established, local land offices have not been created to facilitate local people accessing land certificated through the Propriété Privée Non Titrée (PPNT) allowed by the 2006 land reform legislation. Other locally legitimate private lands in the customary tenure system (forested clan land reserves, disused agricultural fields in long fallow) remain unrecognised by either SFR or PPNT systems.

Although community forestry policy in Madagascar is often described by its proponents as being intended to facilitate participation and empowerment, because of its highly technical and bureaucratic processes, it typically remains in the hands of outsiders, while local people mainly stay in their role as passive recipients of project activities as observed in CBNRM and community forest management (CFM) initiatives elsewhere (Leach et al. 1999). In this context, local people are rightly suspicious about the true intentions of foreign entities' interest in Madagascar's biodiversity, and upon becoming the target/recipient of foreign attention they often fear the loss or decrease in access to natural resources (Evers et al. 2006; Pollini and Lassoie 2011; Simsik 2004).

12.4 Discussion

12.4.1 Conservation of a Biodiversity Hotspot

In scientific and conservation literature on the island of Madagascar discussions have been mainly centred on two issues. Firstly that it is bestowed with significant biodiversity unique in its composition and secondly that it simultaneously faces severe economic disadvantage. However, another perspective is apparent and should not be neglected: The lives of people living in rural Madagascar have been exposed to local conditions over long periods resulting in cultural identities, livelihood activities and patterns of daily life, which are intrinsically linked to the environmental and social features of their surroundings. Due to minimal infrastructure, rural areas are far from the political centre of the country and people living in these areas have often developed their own customary rules demonstrated by the various norms that regulate both land tenure and use systems as described earlier in the chapter. Malagasy rural peoples' ideas are, therefore, based on their identity, traditions and belief systems that have been shaped by close interdependence with their environment, and often with minimal involvement with the state. Understandings of natural processes are complex, incorporated in narratives, and often explained locally by spiritual beliefs and as such these local ways of seeing things are deeply embedded within cultural systems. Such systems of course do not all produce results favourable to nature conservation, but there is ample experience that particular sensitivities to ecological processes may be understood in local knowledge and folklore and have often been integrated into customary rules.

After the environmental policies of pre-colonial Merina monarchs, and the reserves established by French colonial conservationists, the recognition of Madagascar as a global priority through designations such as "Biodiversity Hotspot" has led to huge increases in financial inflows from diverse international donors for conservation activities – particularly over the last 2 decades. With the relatively simplistic portrayal of inherently valuable biodiversity being threatened by anthropogenic activities, conservation organisations have introduced moral standards of developed countries to the island. These standards have led to the establishment of many new protected areas in order to conserve rare species and habitats within natural wildernesses from the Malagasy people who are seen as threatening them. Initially, the protected areas were designed and implemented with dominant roles for expatriate technicians and scientists, but recent years have seen an increasing consideration of socio-economic, cultural factors and a decreasing role of expatriates as Malagasy technicians' capacities have been enhanced and fill more of the prominent roles.

Despite these improvements full consideration of how cultural characteristics should be dealt with remains a huge challenge, since the points of origin of conservation and of Malagasy culture are fundamentally different from each other. Surely, one of the most important challenges for conservationists and Malagasy people is finding ways to bridge these different perspectives.

There are an exceptional number of anthropological studies in Madagascar highlighting various cultural perspectives of Malagasy rural people. These studies provide interesting insights into Malagasy life and belief systems that have frequently demonstrated the complex interrelation between man and nature of forest people (Peterson et al. 2010). They do however, typically remain somewhat detached from problem solving for conservation often leaving the debates to be framed by the language of economics as the following passage exemplifies:

> protected areas… are described [by anthropologists] as kinds of property (whether territorially or intellectual) and as kinds of resources whose value can be measured, managed, and distributed. (Orlove and Brush 1996: 346).

Kaufmann (2006) attributed the opaqueness of the environmental crisis to a false dichotomy between scholars from Cartesian natural science logics and those from more social science Kantian perspectives in his 2006 special issue of the journal Conservation and Society and subsequent book "Greening the Great Red Island: Madagascar in Nature and Culture" (Kaufmann 2008) he and colleagues argue for conservationists and scientists to consider Madagascar's environment more holistically. Nowadays, conservation organisations do seek to integrate anthropological knowledge into conservation schemes through the engagement of anthropologists (Orlove and Brush 1996) and in starting to tackle the issue of integrating local cultural aspects into conservation initiatives. The integration of the traditional social code of the *dina* into Community Forestry contracts between local associations and the forest administration is a tangible example of such efforts (Andriamalala and Gardner 2010). Another example is the case with the mountain of Angavo (in the Androy Region of the South) that has been recognised by the Malagasy government as a new protected area (Natural Monument – IUCN Category III), which simultaneously recognises local cultural values and integrates the local clan-based organisations into management (Ratsirarson et al. 2009). The aim is to protect these values and the biodiversity contained within the mountain forests from international mining corporations seeking to undertake mineral exploration there. Designation of the mountain, containing sacred sites for the Tandroy people, as a protected area, certainly helps protect the area against foreign extractive activities, but to what extent it also limits local community access to non-sacred areas of forest is an important question. Another issue is that the nature of culture, as dynamic and evolving, is perhaps not dealt with as well as it might be, for example a situation of increasing resource scarcity. Local desires to use previously conserved (but non-sacred) forests may be constrained by their being within a strict conservation zone of the protected area. So while it may seem on the surface that conservation is integrating cultural considerations into its design, there can still remain unresolved discrepancies.

One approach to dealing with this challenge is first of all to distinguish between discrete realms of knowledge among and within different stakeholder groups with an interest in any given area, taking account of the plurality of thoughts and attitudes contained therein, which may lead to a similar multitude of possible solutions. In particular social studies may elucidate traditional knowledge of nature and natural processes, which is an essential complementary form of knowledge to more technical and scientific approaches. An example in Madagascar to draw upon is Styger et al. (2007) who showed that next to their own ecological research findings, interesting insights from traditional knowledge on slash-and-burn farming and its ecological consequences were represented by a clear ecological awareness at the local level, sometimes more nuanced and appropriate than the scientific ones. The same has been identified by other social science studies on environmental consciousness, e.g. Simsik (2004) and Fritz-Vietta and Stoll-Kleemann (in preparation). Such integration of local and scientific approaches is valuable in striving to develop suitable hybrid solutions for conservation policy. This concept is illustrated in Fig. 12.2.

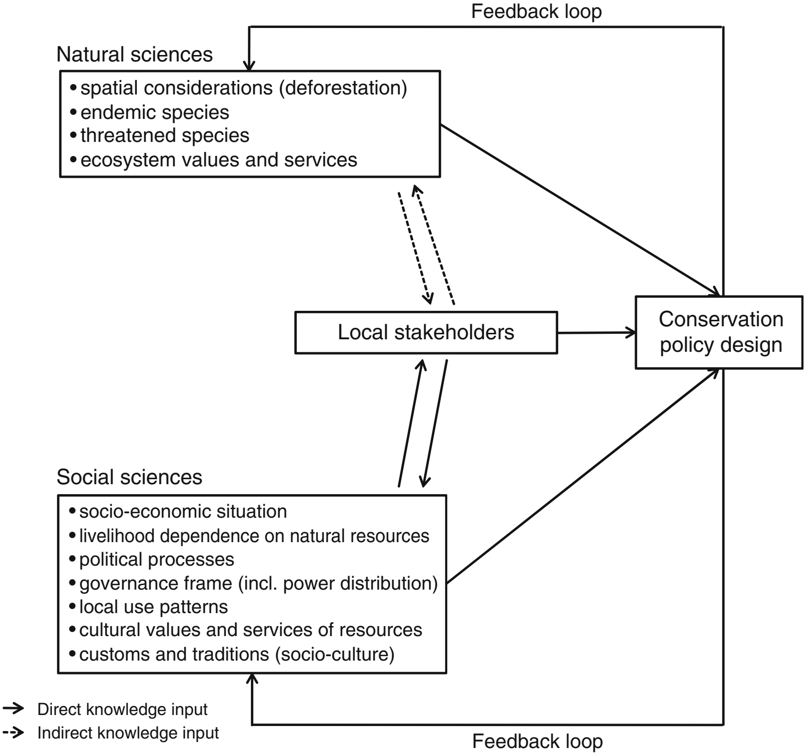

Fig. 12.2 Reconciliation of natural and social science for conservation policy

Sayer and Campbell further reinforce this necessity of establishing more integrated knowledge systems in their book “The science of sustainable development: local livelihoods and the global environment” (2004) where they emphasise connections between natural and social sciences, and local knowledge of site-based management stakeholders.

12.5 Conclusion

A fundamental change of conservation ideology has to happen, if conservation is to support the people in Madagascar while saving their island’s unique biodiversity. This will only be possible, if scientific disciplines can move beyond their traditional research approaches and engage in more collaborative research processes, which combine insights from diverse disciplines and forge deeper relationships between researchers, communities, practitioners and the policy makers, lobbyists and donors who are driving conservation. Just as the classical divide between nature and culture does not apply in Malagasy rural contexts (just as in fact it does not anywhere else in the world), and it can, therefore, not constitute the sole basis for design and delivery of conservation activities. So next to ecological values, equity, justice and autonomy should be fundamental drivers of conservation initiatives in Madagascar. We need to move beyond the simplified portrayals of conservation from the pure ecological and social dichotomy to a situation where we have the capacity to integrate "the social" into conservation from the identification of objectives to the design and delivery of strategies. New concepts have to replace the traditional way of classifying local phenomena, meaning that for example the category "people of marginal groups" implies in principle that people lack particular capacities and are at the edge of the society; instead it is more helpful to identify their strengths and the ways they adapt to their situation, assuming that everyone can develop power and means to handle peculiar living conditions while these provide them with particular opportunities for alternative livelihoods. And also that conservationists should increasingly use unconventional means of understanding knowledge systems which are unfamiliar to them, this could include taking part and promoting more artistic and creative activities such as dance, songs, spiritual ceremonies and storytelling as well as more conventional mechanisms and approaches based on household economics, and agricultural and forestry systems.

So it seems that conservation policy implementation will only succeed if community connectedness across all stakeholders is achieved and the new governance arrangements which are established are open, trusting, accommodating, flexible and sharing (O'Riordan 2002). Clear language, listening and the sharing of interpretations is a joint endeavour and has the potential to strengthen the sense of collective working and can harmonise knowledge exchange among the various parties. However, in order to build confidence, boundaries of familiarity need to be crossed through establishing new alliances stretching across academic disciplines, policy makers, practitioners and the local people concerned by conservation.

Finally, we recommend that conservationists become more open about what they are really offering for Malagasy communities to negotiate in terms of their rights to use natural resources and have their customary land ownership recognised. Said in another way this means heeding the recent call of McShane et al. (2010) for more transparency by conservation organisations in disclosing and negotiating the real trade-offs at play in conservation. At the same time scholars who are critical of the social justice issues around Malagasy conservation could do well to find more creative means to addressing their concerns than solely producing more literature (Brockington and Duffy 2010). Perhaps we need to consider how we can all step out of our comfort zones to better reconcile differences and to find new ways of working to achieve effective and equitable conservation for the biodiversity and people of hotspots like Madagascar.

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Chapter 13
The Kingdom of the Frogs: Anuran Radiations in Madagascar

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Abstract The island of Madagascar harbors one of the world's most diverse amphibian faunas with an outstanding degree of 100% endemism at species level among the over 270 native species of frogs. The high research activity of recent years, together with the use of integrative taxonomic approaches, combining molecular genetics, comparative morphology, and bioacoustics, has led to the identification of many morphologically cryptic but evolutionarily highly divergent species of Malagasy frogs, leading to estimates of over 200 yet undescribed species. Ongoing phylogenetic and phylogeographic studies aim to understand the processes that might have generated this unique species diversity and microendemism. By now the larval stages of many Malagasy frogs are tremendously underexplored, although their relevance for the evolution, ecology, and conservation of animals with a biphasic lifestyle is apparent. Habitat destruction and fragmentation are the most important factors threatening amphibian diversity in Madagascar.

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13.1 Introduction: Diversity of Malagasy Amphibians

Extant amphibians – the subclass Lissamphibia – experienced an impressive increase in recognized species numbers in the past two decades at a global scale. Whereas the number of new species descriptions in the last decade of the twentieth century was 810 (Köhler et al. 2008), this number increased to nearly 1,200 descriptions of new amphibian species in the first decade of this century, equaling an increase in the description rate of 48% from one decade to the next (Fig. 13.1). These discoveries, in amphibians, are by no means a result of taxonomic inflation, e.g., due to changing species concepts (Köhler et al. 2005). Instead, many of the newly described species were formerly unknown from collections and represent "true" discoveries as a result of intensified fieldwork in poorly explored areas, mostly in the humid tropics. Furthermore, the accumulation of molecular data sets and the increasing use of integrative taxonomic approaches combining molecular genetics, comparative morphology and bioacoustics revealed additional evidence for an underestimation of the actual species richness and allowed for a proper delimitation of cryptic but divergent species, as well as to identify complexes of

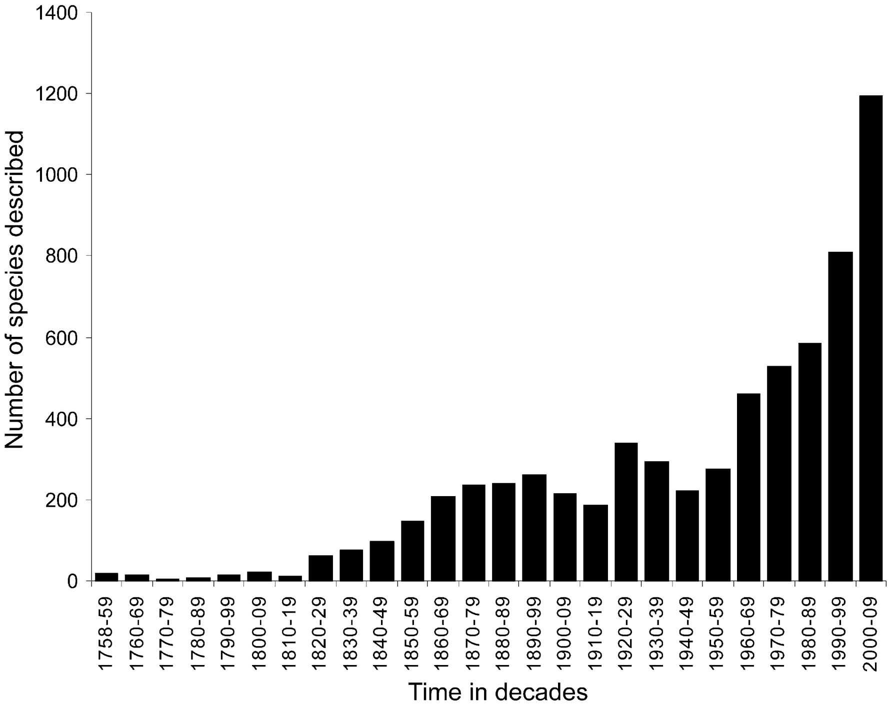

Fig. 13.1 Descriptions of new amphibian species per decade from 1758 until the end of 2009 at a global scale (including taxa considered to represent valid species today only). Note that there is a steady increase in description rates recognizable since 1940. Most of the species discoveries originate from the humid tropics, particularly the Neotropics

species hidden under a single scientific name (Vences and Wake 2007; Padial et al. 2009; Vieites et al. 2009). As a result of these developments, the total number of recognized valid amphibian species accumulated to approximately 6,600 at the end of 2009 (AmphibiaWeb 2010).

Madagascar has been long recognized as one of the world's highest priority hotspots for biodiversity conservation and one of the top megadiversity countries (Myers et al. 2000). Considering its surface area (587,000 square km), with currently 273 officially recognized frog species (Glaw et al. 2010; Köhler et al. 2010; Vences et al. 2010) Madagascar harbors a remarkable portion of the global species richness of anurans (frogs), whereas caecilians and salamanders are absent from the island. Current species numbers have doubled since 1991 when only 133 described species were recognized in the monograph of Blommers-Schlösser and Blanc (1991). Estimates of the true amphibian diversity, however, are still preliminary. Based on an integrative approach of molecular, morphological, and bioacoustic characters, another almost two-fold increase in species numbers to a minimum of 373 and up to 465 species is anticipated (Vieites et al. 2009). This amazing explosion of recognized species diversity is unparalleled and would elevate Madagascar among the top five most diverse countries on the planet for amphibians, together with Brazil, Colombia, Ecuador, and Peru, but this high rank may level off again as also from other tropical countries high proportions of unrecognized amphibian species are expected. The global importance of Madagascar's amphibian fauna is nevertheless outstanding, especially regarding its extreme degree of endemism at species level (100%). Only two species are considered to be nonendemic: the introduced *Hoplobatrachus tigerinus*, and the widely distributed *Ptychadena mascareniensis*, which has been reported also from mainland Africa. Interestingly, molecular studies have shown that the *P. mascareniensis* populations from Madagascar are noticeably differentiated from the ones that so far have been studied from the African mainland, and probably represent a different species (Vences et al. 2003, 2004). Based on molecular studies, native Malagasy amphibians are represented by four families of frogs: Mantellidae, Microhylidae, Ptychadenidae, and Hyperoliidae (Fig. 13.2), which can be subdivided in five major lineages of independent origin with 100% species-level endemism (Vieites et al. 2009; Glaw and Vences 2006, 2007).

The origins of these five lineages of extant Malagasy amphibians are still poorly known, and virtually no fossils have been discovered that would help to understand their evolution. The early (Triassic) history of frogs has been based on one famous fossil (*Triadobatrachus massinoti*) from northern Madagascar that is the oldest Malagasy fossil that can be considered as an ancestor of living frogs (Rage and Roček 1989). From the Late Cretaceous, fossils of a giant frog named *Beelzebufo ampinga* are known that might be related to South American ceratophryids (Evans et al. 2008) but this species probably bears no closer relationships to any of the extant lineages today present on Madagascar. The current consensus is that many endemic vertebrate lineages of the island resulted from overseas dispersal of African founder individuals during the Cenozoic, from 65.5 million years ago (mya) to the present, whereas others are relicts of the late Jurassic to upper Cretaceous

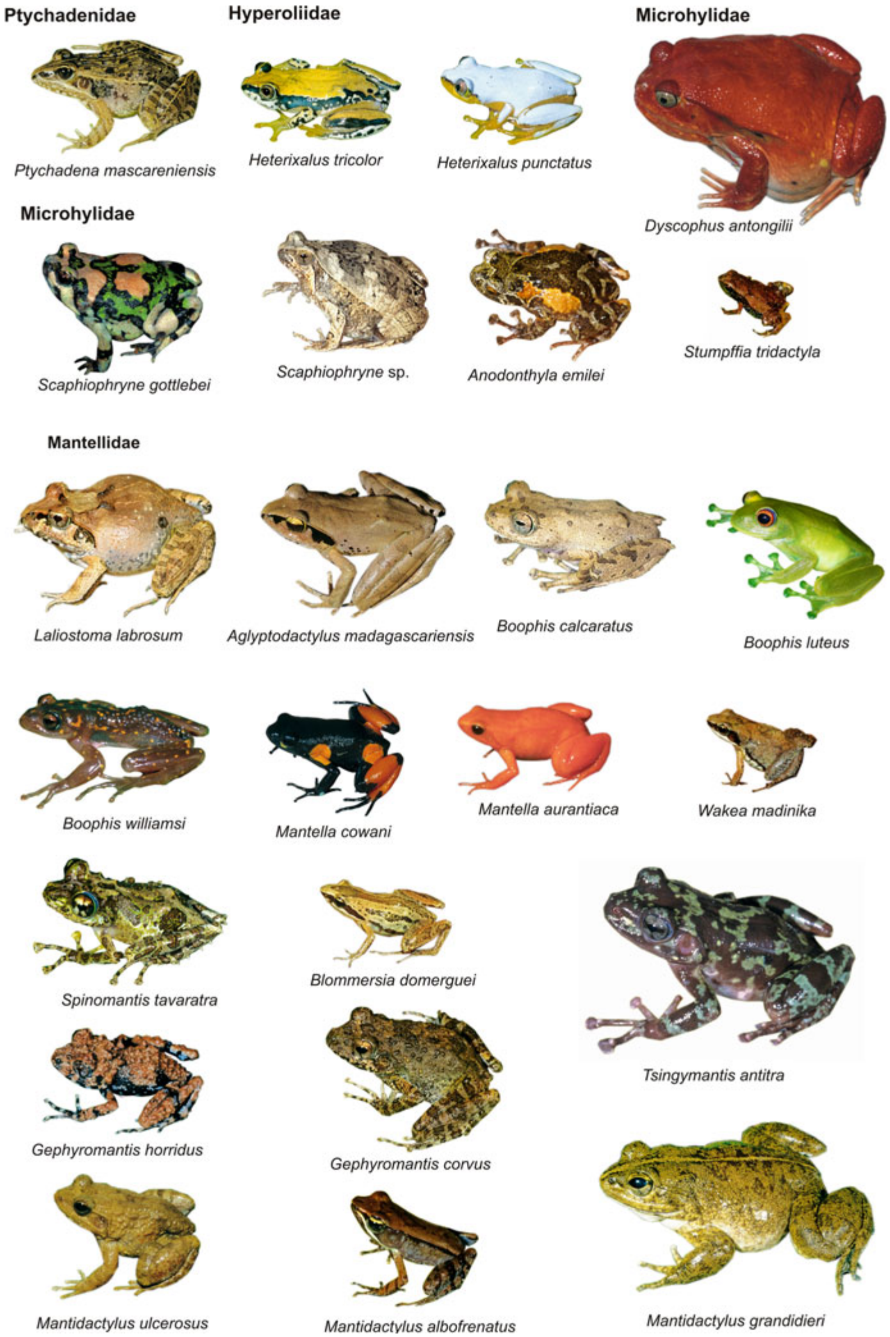

Fig. 13.2 Overview of diversity of Malagasy amphibians. Size of pictures reflects relative size (small–large) of the species, but photos are not to scale (size differences in reality are much larger, with up to 100 mm for *Mantidactylus grandidieri* and about 10 mm for *Stumpffia tridactyla*)

fragmentation of Gondwana during which Madagascar separated from Africa 183–158 mya, broke free from India some 88 mya, and have been isolated ever since (Yoder and Nowak 2006). Radiations of these Malagasy lineages resulted in a wealth of endemic species, many of which are also microendemic to small ranges within the island. Malagasy amphibians contain species of late origin that almost certainly originated through dispersal (hyperoliids and *Ptychadena*) as well as older groups with ages of origin of 50–70 mya (mantellids and two lineages of microhylids). These latter groups are of less-obvious origins but may have dispersed from Asia (Van der Meijden et al. 2007).

The Mantellidae is the largest family of Malagasy frogs both in terms of species richness and diversity in morphology, ecology, and reproductive modes. Mantellids comprise three major and well-defined lineages that correspond to the three subfamilies Boophinae (genus *Boophis*), Laliostominae (genera *Aglyptodactylus* and *Laliostoma*) and Mantellinae (genera *Blommersia, Boehmantis, Gephyromantis, Guibemantis, Mantella, Mantidactylus, Spinomantis, Wakea*, and perhaps *Tsingymantis*). Molecular data have provided strong evidence that all taxa included in the Mantellidae form a monophyletic group, and that their sister group is the Asian family Rhacophoridae. Molecular dating suggests that the Mantellidae originated around 58 mya (Glaw and Vences 2007; Vences et al. 2003).

As a general trait, all representatives of the subfamily Mantellinae are characterized by a derived reproductive behavior in which no amplexus occurs and the male positions itself above the female. Additionally, in all species the eggs are deposited outside of the water. Species in many mantelline genera are characterized by femoral glands that probably are related to their specialized reproduction. Mantellids have evolved many adaptations in life history traits, with species adapted to terrestrial, aquatic, and arboreal habitats (Glaw and Vences 2007; Andreone and Luiselli 2003).

The subfamily Boophinae contains a single genus, *Boophis*. These tree frogs are mainly arboreal, are generally breeding in running water and have a typical larval development. They occur over all major types of habitats in Madagascar. Although the highest diversity of this genus is found in the eastern rainforest, they also include species specialized to xeric conditions in western Madagascar and to high-altitude ericoid vegetation above the tree line.

The two genera of the subfamily Laliostominae, *Aglyptodactylus* (three species), and *Laliostoma* (one species), are mainly terrestrial and breed in temporary ponds, often explosively in large aggregations. Whereas *Laliostoma* is a typical species of the arid western habitats, *Aglyptodactylus* are common in eastern rainforests as well as in western deciduous forests.

Microhylidae are represented by the three subfamilies Cophylinae (genera *Anodonthyla, Cophlya, Madecassophryne, Platypelis, Plethodontohyla, Stumpffia*, and *Rhombophryne*), Dyscophinae (genus *Dyscophus*), and Scaphiophryninae (genera *Paradoxophyla* and *Scaphiophryne*). Relationships among the various lineages of microhylids are not yet well-resolved, but molecular data indicate that the Cophylinae and Scaphiophryninae together form a monophyletic lineage with an age of around 50–60 mya (Van der Meijden et al. 2007; Wollenberg et al. 2008). The origin of the Dyscophinae in Madagascar is apparently independent from the other microhylid groups, although they are estimated to be of similar age

(50–60 mya). Dyscophinae are rather related to groups of Asian microhylids (Van der Meijden et al. 2007).

Most cophylines are closely tied to rainforest habitats and have a reproduction characterized by parental care. Within this group a huge variety of life history traits exist, with arboreal, terrestrial-fossorial, and miniaturized terrestrial forms (Glaw and Vences 2007; Andreone et al. 2004). The genera *Dyscophus*, *Paradoxophyla,* and *Scaphiophryne* are somewhat different from cophylines in their habitat preferences, living mainly in open areas and with some species occurring in the arid and subarid conditions of western and south-western Madagascar. Most of them are mainly terrestrial, although some species are partly rupicolous (Glaw and Vences 2007; Andreone and Randriamahazo 2008b).

The endemic genus *Heterixalus* is the only group of the Hyperoliidae on Madagascar, comprising eleven species which inhabit grassland, rice fields, and forest edges. They are quite similar in habitat preferences and general behavior to other hyperoliids from mainland Africa, probably due to the fact that *Heterixalus* are quite closely related to the African genus *Afrixalus*. Molecular studies have corroborated that the ancestor of *Heterixalus* reached Madagascar about 22 mya, and probably from Madagascar, the ancestor of *Tachycnemis* (an endemic, monotypic genus of hyperoliids from the Seychelles) dispersed to the Seychelles (Vences et al. 2003; Wollenberg et al. 2007).

13.2 History of Discovery and Prospective for Species Inventory of Madagascar's Amphibians

The history of exploration of the Malagasy amphibian fauna is characterized by alternating periods of low and high research activity, with the periods of intensive research assignable to a few outstanding scientists (see Köhler et al. 2005 for respective names and periods). Consequently, a trend in species description rates is less evident in Madagascar when compared to the general global increase (e.g., Köhler et al. 2008). However, it is remarkable how the period of the 1980s, with only two frog species described within the whole decade, was followed by a boost in species discoveries with an increasing tendency (Fig. 13.3). As evaluated by Vences et al. (2008), traditional comparative morphology of preserved specimens tends to identify only a small portion of the actual species richness. Köhler et al. (2005) and Vieites et al. (2009) showed that the molecular differentiation of newly described species, and newly identified candidate species (a term proposed by Vences and Wake 2007), is at similar levels as between described and well-established species of Malagasy frogs. This indicated that the increasing number of species are not the result of taxonomic inflation (e.g., elevating subspecies to specific status) but rather due to the application of integrative taxonomic approaches as mentioned in the introduction.

The high research activity of recent years has led to the identification of many more species of Malagasy frogs than there are names available. In consequence of

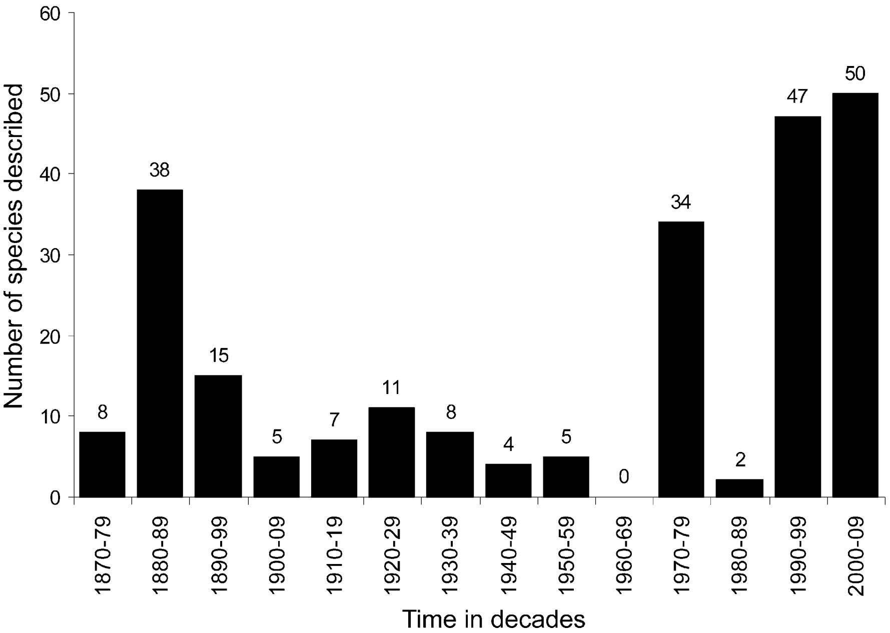

Fig. 13.3 Descriptions of new Malagasy amphibian species per decade from 1870 until the end of 2009 (including taxa considered to represent valid species today only). Prior to 1870, nine frog species have been described from Madagascar (not included here)

this, Vieites et al. (2009) classified the yet undescribed frog species and lineages from Madagascar in three categories (1) confirmed candidate species (CCS) are those differing clearly by morphological and bioacoustic characters and usually showing high genetic differentiation that are hypothesized to be distinct species to be newly described or resurrected from synonymy; (2) unconfirmed candidate species (UCS) are deep genealogical lineages (bioacoustically and morphologically unstudied and usually derived from geographically distant populations) for which general indications exist that they might be distinct, undescribed species; and (3) deep conspecific lineages (DCL) are deeply divergent genealogical lineages, studied but not having clear morphological or bioacoustic differences with described species (Vieites et al. 2009).

Undescribed diversity is phylogenetically widespread in Malagasy frogs, is not restricted to morphologically cryptic clades, and occurs throughout Madagascar both in poorly explored and in better-studied areas. Vieites et al. (2009) found candidate species in most clades except in a few monotypic or species-poor genera (e.g., *Dyscophus* and *Wakea*). Genera such as the colorful *Mantella* or *Heterixalus* are rather well-studied and consequently contain only a few candidate species, whereas in the three most speciose and diverse clades (*Boophis*, *Mantidactylus*, and Cophylinae), the number of candidate species is close to or even exceeds the number of described species (Vieites et al. 2009). Additional to that, many described species contain significant divergent DCLs, and how these should be considered in ecological, evolutionary, and conservational studies remains ambiguous.

Completing the species inventory of Madagascar's amphibians – similar to the situation at a worldwide scale – is a relevant prerequisite for conservation assessments and thus should be accelerated with urgency. Increasing the rate of species descriptions of Malagasy anurans nowadays is rarely a problem of identification, but a matter of the number of scientists working on this task and the time available to them to produce manuscripts with scientific descriptions. The current decade will probably be devoted to describe most of the already identified nameless species, but since each field survey reveals additional samples of new candidate species, there is barely an end of species discoveries in prospect. Taking into account that also the intensity of amphibian surveys in Madagascar is still limited by time, personnel, and financial resources (D'Cruze et al. 2009), and that this fact is accompanied by an ongoing rapid habitat loss, efforts apparently need to be further intensified to obtain a satisfying inventory of Madagascar's actual amphibian diversity.

13.3 Phylogeographic Diversity and Speciation Patterns of Malagasy Amphibians

Most described Malagasy amphibian species are only known from one or just a few localities and have not been found elsewhere. This pattern is also consistent among the undescribed species; only 6 of the 219 CCS and UCS are widespread, whereas 63 are currently known from small ranges and 154 from single localities (Vieites et al. 2009; Glaw and Vences 2007). Despite this high level of microendemism, the different lineages of frogs are unevenly distributed in the different climatic regions of Madagascar and most of these differences are probably due to the limited ability of some groups to survive in arid habitats. Madagascar's bioclimatic zonation follows a primary east-west (wet-dry) division and as it can be expected in a group with a life usually linked to water and humidity, most species of amphibians are distributed in the moist evergreen rainforests along Madagascar's east coast. Divergence among populations specializing to the humid east and dry west has been hypothesized to be one mechanism of species formation in Malagasy vertebrates. This is supported by the distribution of some Malagasy anuran sister species widespread in eastern and western Madagascar (e.g., *Boophis tephraeomystax* vs. *B. doulioti*). The underlying process would be adaptive, with the sharp ecological distinction between eastern and western habitats constituting a barrier to gene flow and causing a basal split between eastern and western clades in the phylogeography of species of initially wide distribution, eventually leading to speciation. Yoder and Heckman (2006) refer to this hypothesis as the "ecogeographic constrain". But recent studies have suggested that this traditional perspective on its biogeography cannot explain all the variety of phylogeographic differentiation found across different taxonomic levels (e.g. Wilmé et al. 2006; Yoder and Heckman 2006; Boumans et al. 2007).

To understand the processes that might have generated the species diversity and microendemism of Malagasy amphibians, it is useful to look more closely at the spatial patterns of species distributions. The highest numbers of species occur in the central east, centered in areas between the latitudes of Andasibe and Ranomafana. Here, some localities are known where more than 100 species of frogs occur sympatrically in rather small areas (Glaw and Vences 2007). This concentration of species diversity in the central east is probably influenced by the fact that this area coincides with especially well-sampled localities (Andasibe and Ranomafana; Vieites et al. 2009) but possibly also caused by a random statistical phenomenon known as the mid-domain effect (MDE): If distribution areas are randomly plotted on a certain area, the highest degree of overlap of distribution areas will be in the center (Lees et al. 1999; Colwell and Lees 2000). In Madagascar, the highest species diversity of amphibians, and of various other groups of organisms, is not only found at mid-latitudes but also at mid-altitudes, peaking between 800 and 1,000 m above sea level (Vences et al. 2009).

Another general phylogeographic tendency in Malagasy anurans (especially in different cophyline lineages, but also in subgroups of *Gephyromantis*) is that species diversity and microendemism are highest in the mountainous regions of northern and north-eastern (e.g., genera *Cophyla, Platypelis, Rhombophryne,* and *Stumpffia*) and south-eastern Madagascar (e.g., genera *Anodonthyla* and *Madecassophryne*) (Wollenberg et al. 2008; Glaw and Vences 2003). This is in agreement with a hypothesis of mountainous areas as historical centers of clade origin and speciation in Madagascar (Raxworthy and Nussbaum 1995; Wollenberg et al. 2008) because both adaptive and vicariant speciation are likely to be favored in these areas (Vences et al. 2009). Under a vicariant scenario, the higher elevational heterogeneity of the north might have allowed northern massifs to successfully act as refuges during climatic shifts such as the Pleistocene glaciations (Wollenberg et al. 2008), which triggered globally fluctuating temperatures with drier and more humid periods in Madagascar (Wilmé et al. 2006).

A similar process may also have triggered speciation in western relicts of humid forests. Of the amphibian species today occurring in arid western and south-western Madagascar, many are restricted to humid refugia such as Isalo or the karstic limestone massif of the Tsingy de Bemaraha. Only relatively few species are specialized to the areas of deciduous forests in the west, and even fewer to open areas of spiny forest or open landscape, like the wide savannahs in the island's interior. In several cases, the species endemic to humid relict forests in the west are known to be sister to widespread eastern species, such as *Boophis tampoka* from Bemaraha, which is closely related to the eastern *Boophis luteus*, and may have diverged after dispersing through a humid corridor to Bemaraha in the past. Evidence for the existence of such past connections between humid relict forests in the west and the main eastern rainforest band are obvious from a significant number of frogs occurring at the western Isalo massif (e.g., *Boophis luteus*, *B. obscurus, Mantidacytlus femoralis*, and *M. lugubris*) that are apparently conspecific with those of eastern Madagascar (Glaw and Vences 2007). Since it appears very unlikely that these frogs were able to reach the Isalo Massif by traversing large arid barriers, this pattern may indicate that the forest remnants in Isalo were still connected with the eastern rain forest in quite recent time.

Finally, it should be emphasized that the quality of biogeographic analyses strongly depends on the quality of the underlying taxonomic and distributional data. For a large proportion of the Malagasy amphibian fauna, such data are still insufficient. The integration of "classical" methods, such as similarity indices between faunas, with molecular phylogeographic studies will help to reconstruct much of the past dispersal and vicariance processes within Madagascar. Further research is also needed to understand the origin of the high degree of microendemism in Madagascar. There is some evidence that the restriction of taxa to small distributional areas might be influenced by the evolution of specialization to particular environments (and thus reduced dispersal ability in areas with heterogeneous environments) that might be typical of tropical as opposed to temperate regions.

13.4 Morphological Diversity and Ecology of Malagasy Tadpoles

When discussing amphibian diversity, most studies focus on the adult stages. However, the larval stages – tadpoles – of frogs occupy entirely different niches compared to the metamorphosed frogs. They are typically aquatic and microphagous suspension feeders, and their relevance for evolution, ecology, and conservation is tremendously underexplored.

Larval stages of many Malagasy amphibians are poorly known and within the 273 described species and the approximately 200 undescribed candidate species (Vieites et al. 2009), currently there are tadpoles described for only about 70 species. Nowadays, identification of Malagasy tadpoles is based on DNA barcoding (Thomas et al. 2005) and the larvae of about 100 species are in the process of description (e.g., Randrianiaina et al. 2011).

Developmental modes in Malagasy amphibians can be classified in endotrophic modes (i.e., tadpoles obtaining their energy from their yolk reserve), or exotrophic modes (i.e., energy obtained via food uptake from the environment). Two kinds of endotrophic development were assumed to exist on Madagascar; direct development and nidicolous tadpoles. Most of the terrestrial cophyline microhylids reproduce in jelly nests or foam nests with nonfeeding (nidicolous) tadpoles, whereas in the arboreal cophyline species, these equally nidicolous tadpoles are free swimming in leaf axils of plants or water-filled tree holes (Glaw and Vences 2007). Some mantellid species of the genus *Gephyromantis* have been reported for a long time to be direct developers (Blommers-Schlösser 1979), but this could be confirmed only insufficiently so far. For some of these *Gephyromantis* species, the observation of nonfeeding larvae in a terrestrial jelly nest (in a *Gephyromantis* candidate species close to *G. blanci*) and in streams (e.g., in *G. tschenki*; Fig. 13.4) evokes questions about the developmental mode in several *Gephyromantis* subgenera.

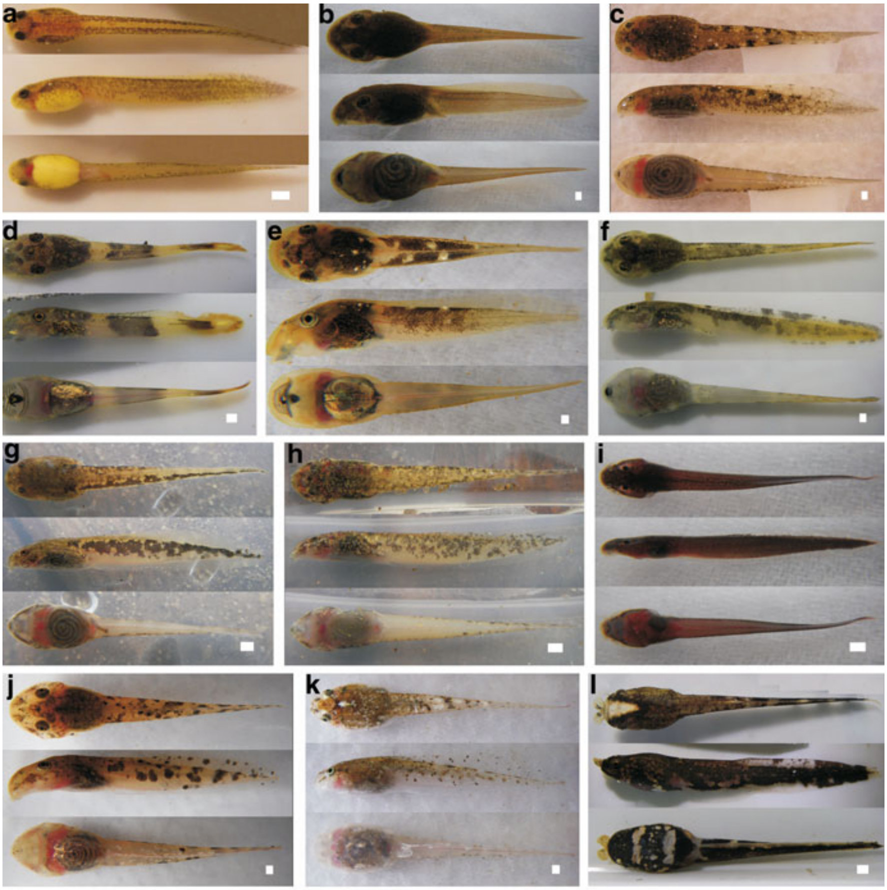

Fig. 13.4 Diversity of tadpoles in the family Mantellidae (dorsal, lateral and ventral views of live specimens): (**a**) *Gephyromantis tschenki*, (**b**) *Boophis periegetes*, (**c**) *Spinomantis* sp. 2, (**d**) *Boophis schuboeae*, (**e**) *Boophis marojezensis*, (**f**) *Gephyromantis azzurrae*, (**g**) *Mantidactylus femoralis*, (**h**) *Mantidactylus mocquardi*, (**i**) *Mantidactylus cowanii*, (**j**) *Mantidactylus majori*, (**k**) *Boophis picturatus*, (**l**) *Mantidactylus aerumnalis*. The scale bars represent 1 mm

The majority of Madagascan frogs show an exotrophic developmental mode. They occur in all kinds of water bodies, even outside the forest in rice fields and sometimes in temporary stagnant water. However, compared to other parts of the tropics, a particularly high proportion of Madagascar's tadpoles live in streams where they are of prime ecological importance. Tadpole developmental time varies from 10 days for explosive breeders living in the dry west (Glos et al. 2007) to probably several years for the species occurring at very high altitudes in central Madagascar (e.g., *Boophis williamsi*).

Except for a few remarkable tadpoles (Fig. 13.4), e.g. *Boophis schuboeae* (Glos et al. 2007), *Boophis picturatus* (Grosjean et al. 2011) , and *Mantidactylus cowanii*

(Altig and McDiarmid 2006), and in general microhylids (see Grosjean et al. 2007), the majority of Malagasy tadpoles has a rather similar body shape and usually they share similar habitat requirements. Morphological variability mostly affects the components of the mouth of the tadpole (labial teeth, jaw sheath, and papillae) allowing a morphological grouping of at least twelve major ecomorphological guilds among exotrophic Malagasy tadpoles (Fig. 13.5): (1) Generalized tadpoles show the typical oral disk of tadpoles with keratinized tooth and jaw sheath, and between 2 and 8 upper (of which usually only one is continuous) and 3 lower labial tooth rows (LTRs). They are found in the mantellid genera *Aglyptodactylus*, *Blommersia*, *Boophis*, *Gephyromantis*, *Guibemantis*, *Laliostoma*, *Mantella*, *Mantidactylus*, *Spinomantis,* and *Tsingymantis*, as well as in *Ptychadena* and

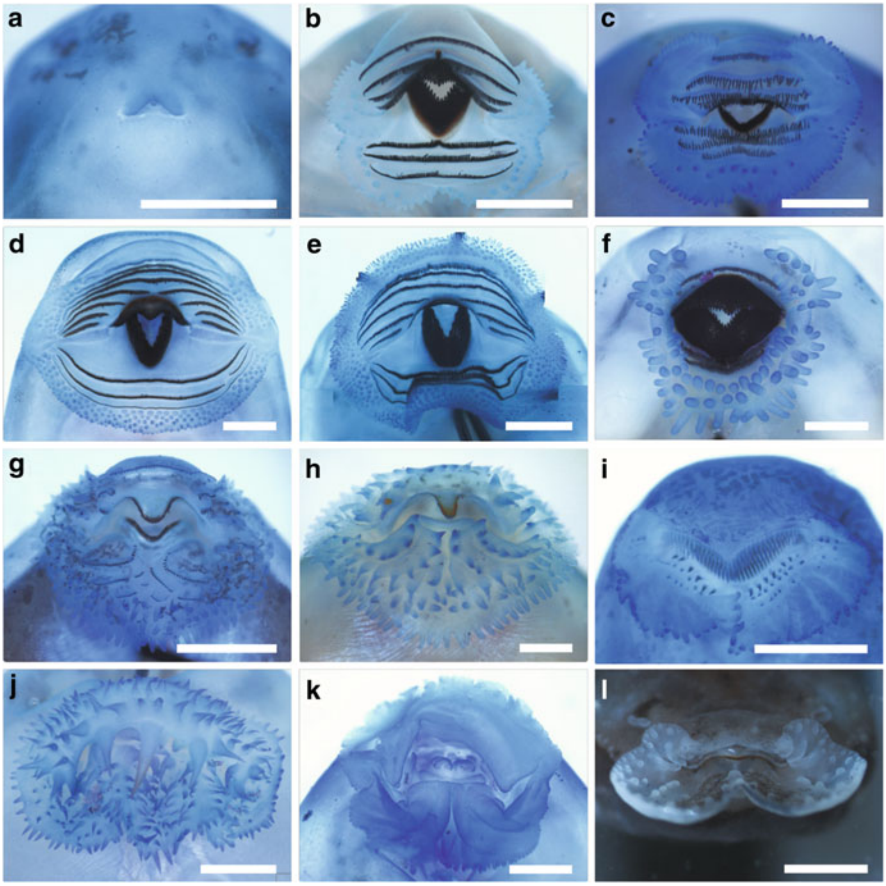

Fig. 13.5 Diversity of oral disk structures in tadpoles of the Mantellidae (stained with methylene blue): (**a**) *Gephyromantis tschenki*, (**b**) *Boophis periegetes*, (**c**) *Spinomantis* sp. 2, (**d**) *Boophis schuboeae*, (**e**) *Boophis marojezensis*, (**f**) *Gephyromantis azzurrae*, (**g**) *Mantidactylus femoralis*, (**h**) *Mantidactylus mocquardi*, (**i**) *Mantidactylus cowanii*, (**j**) *Mantidactylus majori*, (**k**) *Boophis picturatus*, (**l**) *Mantidactylus aerumnalis*. The scale bars represent 1 mm

Heterixalus. (2) The adherent tadpoles of some *Boophis* are characterized by the presence of a dorsal gap in their rows of marginal papillae. They have a rather high number of papillae and between 7 and 9 upper LTR of which 3–5 are continuous, and 3 lower LTR. (3) The suctorial tadpoles of *Boophis marojezensis* and *Boophis vittatus* are characterized by the absence of a dorsal gap of marginal papillae, the presence of numerous small papillae, and by 4 out of 8 upper LTR being continuous. (4) The carnivorous tadpoles known so far from three species of *Gephyromantis* (subgenus *Phylacomantis*) are specialized by having a hypertrophied upper jaw sheath and elongated papillae. They have 2–3 upper and 1–3 lower LTR. (5) Tadpoles with reduced oral structures but with labial teeth belong to *Mantidactylus* (subgenera *Ochthomantis* and *Maitsomantis*) and *Boophis* (*B. majori* and *B*. sp. 35). They are characterized by reduced keratinization of the oral disk. They have moderately sized papillae and 2–3 upper and 3 lower LTR. (6) Tadpoles with reduced oral structures and without labial teeth are typical for *Mantidactylus mocquardi*. They are characterized by the reduction of the keratinization of their jaw sheaths and the complete absence of labial teeth. (7) Tadpoles in which the jaw sheaths are transformed into many spike-like structures belong to *Mantidactylus* (*Hylobatrachus*). Marginal papillae and upper LTR are absent, three lower LTR are present. (8) Specialized tadpoles in which the upper jaw sheath is transformed into three big thorn-shaped papillae are only known from *Mantidactylus majori*. Labial teeth are absent and many elongated and pointed papillae exist. (9) Tadpoles attaining the highest level of the reduction by loosing all the typical keratinized components of the oral disk (LTRF 0/0) are only found in *Boophis picturatus*. (10) Funnel-mouthed tadpoles are specific for *Mantidactylus,* subgenus *Chonomantis*. They are characterized by an upward oriented, umbelliform oral disk that is shaped by an extended lower lip, the oral disk is usually without labial teeth and papillae. Tadpoles of all species in this subgenus are morphologically very similar. (11) Filter-feeding tadpoles are typical for many representatives in the pantropical family Microhylidae and in Madagascar are known from the genera *Dyscophus* and *Paradoxophyla*. These tadpoles live in lentic waters and completely lack jaw sheath, labial teeth, and oral papillae. (12) The microhylid genus *Scaphiophryne* has enigmatic tadpoles without labial teeth but with weakly developed jaw sheaths that have been described as belonging into a psammonektonic guild (Mercurio and Andreone 2006; Grosjean et al. 2007).

One of the world records held by Malagasy amphibians is the enormous species diversity and specimen abundance of tadpoles in the communities of the eastern rain forests. Streams in this region harbor the worlds most species-rich tadpole assemblages, reaching 22 (Ranomafana NP) to 28 species (An'Ala; Vences et al. 2008) in 30 m stretches of a single stream. It is likely that this diversity is caused by two reasons (1) there is only a low availability of stagnant water bodies, which provided an evolutionary advantage for species specializing to reproduce in streams, and (2) due to the virtual absence of fish in tributary streams in rainforests at elevations of roughly >800 m above sea level, an important group of tadpole predators is missing. This latter argument is supported by the fact that, in contrast to other places in the world, the highest numbers of species co-occur in the largest brooks with slow velocity and low canopy cover. Despite the high species richness in the main reproductive season (wet season, January to April) which is also accompanied by very high abundances, these communities are not characterized by competition and show only little functional redundancy (Strauß et al. 2010). The high number of stream-breeding frogs, especially of stream-breeding tree frogs, appears to be a characteristic that distinguishes frog communities in Madagascar from those in other rainforests across the globe.

Even in the dry season (May to July), frogs in eastern rainforests continue to reproduce and stream tadpole communities remain species rich, but the unfavorable climatic conditions cause higher functional redundancy and possibly competition. Tadpoles in these communities show a broad diversity of morphology: tadpoles of the generalized guild 1 and guild 2 (e.g., many *Boophis*) and funnel-mouthed tadpoles of guild 10 are very abundant; also tadpoles with reduced oral disk structures (guilds 5 and 9) and suctorial tadpoles (guild 3) can regularly be found. The endotrophic tadpoles of *Gephyromantis* can rarely be observed but their real affiliation to the stream communities is unclear. Most species are found in slow-moving parts of streams with patches of leaf litter, but a few species also occur in rapids.

A more limited number of rainforest species are mainly or exclusively pond breeders, including, e.g., *Aglyptodactylus*, *Blommersia,* some *Boophis, Guibemantis, Paradoxophyla*, and *Mantella*. Several species reproduce outside larger water bodies, e.g., in tree holes (*Plethodontohyla*, *Platypelis*; endotrophic), phytotelmata (some *Guibemantis*; exotrophic) or in ground nests (some *Gephyromantis*; endotrophic). The developmental times of tadpoles from the eastern rainforests are unknown and may last for at least one to three months.

Tadpole communities from the dry west of Madagascar show very different patterns. For example in the Menabe region, frog reproduction and therefore tadpole occurrence is strongly restricted to the wet season and largely depends on temporary ponds. The few tadpoles found in streams usually belong to pond-breeding frogs that deposited their eggs in puddles that were later flooded. Both explosive and prolonged breeders can be found. The majority of frogs deposit eggs directly in the water, only *Mantella* use ground nests very close to ponds and *Blommersia* attach eggs on leaves above the water. The most species-rich tadpole assemblage observed in this region harbor eight species out of 15 present (Glos 2003). They include species like *Aglyptodactylus laticeps*, *Scaphiophryne calcarata*, and *S. brevis*, belonging to the world record holders with a larval developmental time of only 10 days. In general, these species are characterized by phenotypic plasticity. They can respond to early drying of their habitat by accelerated development resulting in smaller tadpoles. Most tadpoles in this region represent the basic type of guild 1 (e.g., *Aglyptodactylus*, *Boophis*, and *Heterixalus*), only few are filter feeders of guilds 11–12 (*Dyscophus*, *Scaphiophryne*). Some types of tadpoles, e.g., funnel-mouthed tadpoles (guild 10) that are very abundant in the rain forests in the east, are completely missing from the dry west.

Studies on tadpoles represent a valuable method for frog surveys, as tadpoles are present for a certain time window, whereas adult sampling often depends, e.g., on short-time weather events. Madagascan tadpoles could also be used to distinguish between species where adults are morphologically cryptic, and, thereby to confirm previous genetic results (Randrianiaina et al. 2009). Furthermore, exhaustive sampling of tadpoles combined with DNA barcoding regularly leads to the discovery of new candidate species, even in well-studied areas (Vieites et al. 2009).

13.5 Monitoring and Conservation of Malagasy Amphibians

The amphibians of Madagascar are highly threatened. An assessment of the IUCN (International Union for Conservation of Nature and Natural Resources) revealed a proportion of 25% threatened species of all 220 assessed species. Six species were listed as Critically Endangered, 31 as Endangered, and 29 as Vulnerable (Andreone et al. 2005, 2008b). The proportion of threatened species in Madagascar is higher than the per-country average of 12%, but lower than in various other amphibian hotspots (e.g., Neotropics, Australia) or at a global scale (32%).

Habitat destruction and fragmentation are the most important factors influencing local extinction in Madagascar (reviewed in Irwin et al. 2010). By the 1950s, 27% of Madagascar was forested and even a conservative estimate of prehuman forest cover suggests that it had already lost half to two thirds (or even more) of its forest. From the 1950s to 2000s the forest coverage decreased by almost 40%, and was heavily fragmented with a reduction in "core forest" (>1 km from a nonforest edge) of almost 80% (Harper et al. 2007). Frog species richness responds in general negatively to fragmentation (Ramanamanjato 2000; Vallan 2000), forming nested subsets of original species communities in fragments. Edge effects are important proximate causes of diversity loss in fragments, possibly via effects on microclimate and edge sensitivity, which is correlated with extinction vulnerability (Lehtinen et al. 2003).

Further, herpetological diversity decreases in highly disturbed areas, e.g., where intense clearing and burning have produced degraded secondary forest, forest mosaic, or plantations (e.g., Glos et al. 2008b). However, when disturbances were low level, and/or sufficiently long ago, no clear effect on diversity was found in rainforest amphibians (Vallan et al. 2004). Species that reproduce independently from running or standing waters, and species with narrow spatial and temporal niches, are most vulnerable (Vallan 2000, 2002; Glos et al. 2008a, b).

Also, warming trends in Madagascar equal or exceed global averages and may be driving species upslope on mountains (Raxworthy et al. 2008). This trend, which however requires thorough confirmation, may threaten montane endemics that are restricted to narrow elevations close to the summits of most of the major massifs in Madagascar.

Finally, several species experience high levels of demand in the international pet trade and subsequent overcollecting. Of the genus *Mantella*, about 230,000 individuals were collected and exported from Madagascar in 1994–2003. This in particular threatens species with diminished habitats and small population sizes, such as the conspicuous *Mantella cowani* or *Mantella aurantiaca* (Rabemananjara et al. 2008), although we reiterate that these effects are of limited importance compared to the prime effects of habitat loss.

In spite of these considerable threats to Malagasy amphibians, there are no recorded extinctions of any frog species from Madagascar. All historically described species have been observed during the past 20 years, and new species are discovered at an exceptional rate. Chytridiomycosis, responsible for population and species extinctions worldwide, is by now absent from Madagascar. However, given the rate of habitat loss and degradation, and the threat of an accidental introduction of amphibian chytrid, extinctions seem inevitable and Malagasy amphibians may be on the edge of a drastic decline. Hence, amphibian conservation efforts in Madagascar have the possibility of being proactive, rather than reactive (Andreone et al. 2008a). Conservation actions should focus on areas of high herpetological species richness or otherwise important areas such as riverbeds and adjacent gallery forests, montane areas, and dry forest (Irwin et al. 2010). Conservation priorities should be on monitoring communities rather than populations of only a few species, on establishing long-term altitudinal transects, and on monitoring possible infections with chytrid (Andreone and Randriamahazo 2008a, 2008b).

13.6 Conclusion

Madagascar's endemic amphibian fauna harbors a remarkable portion of undescribed diversity, which is geographically and phylogenetically widespread and not restricted to morphologically cryptic clades. The use of an integrative approach of molecular, morphological, and bioacoustic characters promises to give a better perception of the existing anuran species diversity and allows a proper delimitation of cryptic but divergent species, as well as the identification of complexes of species hidden under a single scientific name. This approach is very viable especially for the species identification of the still poorly known larval stages of many Malagasy amphibians and represents an essential cornerstone for the study of one of the world most species-rich tadpole communities. Moreover, the integration of "classical" methods, such as similarity indices between faunas, with molecular phylogeographic studies will help to reconstruct much of the past dispersal and vicariance processes within Madagascar. Further research is also needed to understand the origin of the high degree of microendemism in this island. The current decade will probably be devoted to describe most of the already identified nameless species, because completing the species inventory of Madagascar's amphibians is a relevant prerequisite for conservation assessments and thus should be accelerated with urgency, considering the ongoing rapid habitat loss.

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Chapter 14
Hotspots, Conservation, and Diseases: Madagascar's Megadiverse Amphibians and the Potential Impact of Chytridiomycosis

Stefan Lötters, Dennis Rödder, Jos Kielgast, and Frank Glaw

Abstract Worldwide amphibian diversity is threatened through the emergence of the disease chytridiomycosis, caused by the amphibian chytrid fungus. This pathogen apparently is absent from the amphibian hotspot Madagascar. However, an extinction risk assessment based on environmental niche modelling suggests that a major portion of this island is climatically highly suitable to the fungus. This includes regions of high amphibian species richness. Many species have their entire geographic range in such areas and are at the same time predicted to suffer potentially from chytridiomycosis due to their life history traits. Human-mediated dissemination of the chytrid fungus to Madagascar is considered likely. In particular, there may be a high risk of accidental cointroduction via the animal trade. Severe decline and possibly extinction are expected in a postemergence scenario on Madagascar with more than 270 described and numerous undescribed anuran amphibian species under threat. Effective responses to this potential threat might include (1) an increased attention to 'biosecurity', including the consequent implementation of measures to avoid the introduction of the chytrid fungus, (2) the development of breeding procedures for representatives of all major clades of Madagascan amphibians as a 'pre-emergency prophylaxis' and (3) the development of plans for 'emergency response'.

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14.1 Biodiversity Loss Through Diseases

Biodiversity is unevenly distributed across the globe. Several regions have been identified in which both species richness and endemism is particularly high. The persistence of these "hotspots" comprises an essential element in maintaining global biodiversity by focused conservation strategies and natural resource management (e.g., Mittermeier et al. 2004). Although there are tools to minimize direct anthropogenic impact on hotspots (e.g., by designation of protected areas), a range of indirect impacts remains with few mitigation measures available. Emerging infectious diseases (EID) fall within this class of biodiversity threats and, although their effects on wildlife population dynamics and conservation are not new, there has been an alarming pathogen-related increase in species declines during the last decades (e.g., Smith et al. 2009a). Human impact is linked to this phenomenon and the term "pathogen pollution" has been introduced specifically covering anthropogenic dissemination of pathogens across evolutionary or ecological boundaries (Daszak et al. 2000). Recent examples of dramatic biodiversity loss due to EIDs include virus infections in North American birds (Rahbek 2007), infectious cancer in the Tasmanian Devil (McCallum 2008), or fungus-associated mass mortality in North American bats (Blehert et al. 2009).

At the global scale, the emergence of a fungal disease in amphibians (chytridiomycosis) has within the last decade been made responsible for the most severe case of disease-induced biodiversity loss ever observed (Gascon et al. 2007; Fisher et al. 2009). It has been documented that amphibian species have become extinct and will become extinct through chytridiomycosis (e.g., Lötters et al. 2010; Rödder et al. 2010). Currently, amphibians belong to the most threatened of all vertebrates, with approximately one third of the over 6,500 (according to: http://www.amphibiaweb.org) assessed species threatened with extinction (Stuart et al. 2008; http://www.iucnredlist.org/initiatives/amphibians). Noteworthy, it is suggested that diversity in several of the amphibian hotspots has been affected by chytridiomycosis (e.g., Lips et al. 2008). As emphasized in the IUCN Amphibian Conservation Action Plan, new conservation strategies need to be rapidly implemented to prevent large-scale amphibian diversity loss due to chytridiomycosis (Gascon et al. 2007).

14.1.1 Chytridiomycosis and Amphibian Declines

This EID is an epidermal infection by the parasitic amphibian chytrid fungus, *Batrachochytrium dendrobatidis* (*Bd*). This pathogen spreads via motile infectious zoospores in aqueous environments and encysts and grows to reproductive zoosporangia on amphibian skin. Severe infections cause osmoregulatory imbalance in physiologically essential ions and may lead to a breakdown of neurological function causing cardiac arrest and death (Voyles et al. 2009). The origin of *Bd* and its natural host–pathogen system remain unknown but low global molecular diversity indicates that it has rapidly and only recently spread to its present pandemic state (James et al. 2009). Currently, *Bd* is known from more than 1,700 localities in the wild within all continents where amphibians occur and has been detected in over 400 different host species (http://www.spatialepidemiology.net/Bd-maps). It has been suggested that anthropogenic dissemination of *Bd* is likely to play an important role in the panzootic chytridiomycosis. In particular, the international animal trade has been identified as a plausible pathway of dissemination with hundreds of amphibian species being traded annually (Garner et al. 2009). In recognition of its impact on wild amphibian populations, *Bd* in 2008 was implemented on the list of notifiable diseases of the aquatic health code under the World Organisation for Animal Health (http://www.oie.int/eng/en_index.htm). Possible actions and policy changes have been discussed. However, Australia is so far the only country strongly enforcing specific restrictions on *Bd* (Garner et al. 2009).

Chytridiomycosis has been identified as the key causal mechanism in several focal studies of declines and extinctions on a large scale both geographically and taxonomically (e.g., Schloegel et al. 2006; Lips et al. 2008) including so-called enigmatic declines (Lötters et al. 2010) and there is evidence that many more species have been or will be affected (Rödder et al. 2009; Lötters et al. 2010). However, it is not possible to generalize on consequences of *Bd* emergence as substantial interspecific variation in susceptibility has been observed both in nature and under controlled exposure trials (e.g., Blaustein et al. 2005; Smith et al. 2009b). The host response span from highly susceptible species, which have undergone extraordinarily rapid populations declines, to highly resistant species, which live with high prevalence and pathogen load and may serve as *Bd* reservoirs and vectors (e.g., Rollins-Smith et al. 2009; Schloegel et al. 2010).

Recently, Bielby et al. (2008) defined a biotic index and suggested 837 out of 3,976 worldwide anuran amphibians to exhibit the highest risk of *Bd*-related decline or extinction. This was based on biological and life history information. Particularly susceptible species were pointed out to be living at high altitude with an aquatic life stage, having a restricted range and low fecundity. Subsequently, developing an ecological niche model (e.g., Guisan and Zimmermann 2000), Rödder et al. (2009) estimated the worldwide potential distribution of the amphibian chytrid fungus. The authors used the Maxent algorithm to develop a map indicating the occurrence probability of *Bd* based on 365 presence records of this pathogen (taken from http://www.spatialepidemiology.net/bd) and six bioclimatic variables with spatial resolution 2.5 arc min (taken from http://www.worldclim.org) i.e. 'annual mean temperature', 'maximum temperature of the warmest month', 'minimum temperature of the coldest month', 'annual precipitation', 'precipitation of the wettest month' and 'precipitation of the driest month'. These variables were identified as biologically important for *Bd* in previous studies (e.g. Kielgast et al. 2010). Model evaluation via the area under the receiver operating characteristic curve (AUC) revealed a high precision of the modelling efforts (mean training AUC = 0.937, mean test AUC = 0.910 in 100 models each trained with 70% of the records and the remaining 30% used for model testing). The model uncovered regions of different suitability to the pathogen. Applying a rule set of predictions from their spatial analysis and key host life history variables inferred by Bielby et al. (2008), Rödder et al. (2009) prioritized anuran species according to the risk of decline and extinction due to the developing pandemic chytridiomycosis (see Table 14.1). For this purpose, Rödder et al. (2009) derived a risk factor balancing the relative environmental suitability for the chytrid fungus within the range of a species and its susceptibility according to the biotic index derived by Bielby et al. (2008) (Table 14.1). In this risk assessment, the combined index ranges from 0 (no risk) to 1 (high risk) (Rödder et al. 2009). Most of the 837 anuran species, which by their biology and life history show a high predicted susceptibility to *Bd,* occur in regions which at the same time are characterized by high bioclimatic suitability to the chytrid fungus. In total, 379 of them, with the entire geographic range, fall into areas highly suitable to *Bd*. Rödder et al. (2009) considered these amphibians to be the most threatened by the emergence of chytridiomycosis.

14.1.2 Mitigating the Problem: Ex Situ Conservation

Although some susceptible species may survive severe epizootics of chytridiomycosis on long term (Retallick et al. 2004; Murray et al. 2009), it has been stressed that new rapid and highly comprehensive conservation actions are necessary to avoid catastrophic biodiversity loss. Useful measures include revision of animal trade regulations, development and implementation of pathogen hygiene protocols, increasing public awareness at airports and ports, development of risk factors, monitoring and further research (Andreone and Randriamahazo 2008; Weldon and Du Preez 2008). As there is no certain measure to mitigate *Bd* dissemination and transmission in the wild, ex situ conservation has been promoted in the IUCN Amphibian Conservation Action Plan both in nonrange countries and in-range countries but outside the nature (Gascon et al. 2007). Ex situ conservation includes cryobanking of viable biomaterials and short-term conservation breeding. Although the former has had limited success with regard to vertebrates except fishes, there is some experience and potential for amphibian captive breeding in zoos and aquariums (Gascon et al. 2007; Lermen et al. 2009). Conservation breeding has been successfully performed in a few species, e.g., the Mallorcan Midwife Toad (*Alytes muletensis*), Kihansi Spray Toad (*Nectophrynoides asperginis*), or the Panamanian Golden Frog (*Atelopus zeteki*). Numerous programs in zoos, on- or off-exhibit, have been implemented, leaving conservationists optimistic that some amphibian species may survive through short-term conservation breeding (e.g., McGregor Reid and Zippel 2008). Most of them are coordinated by the "Amphibian Ark" of IUCN Amphibian Specialist Group, IUCN Captive Breeding Specialist Group, and the World Association of Zoos and Aquariums. Species prioritization for several countries including Madagascar have been conducted based on species' status (e.g., IUCN Red List category, occurrence in protected habitat, biological distinctness), availability of specimens and general feasibility of ex situ conservation efforts (http://portal.isis.org/partners/AARK/Lists/Prioritization%20workshop%20results/AllItems.aspx).

Table 14.1 List of 234 Madagascan anuran amphibian species as recorded in the IUCN Red List of Threatened Species on 7 July 2009, their IUCN Red List category and geographic range size (taken from http://www.natureserve.org/getdata/amphibianmaps.jsp; accessed 7 July 2009), each followed by its biotic Index (after Bielby et al. 2008), risk factor for threat through extinction due to chytridiomycosis (after Rödder et al. (2009) and its conservation priority according to 'Amphibian Ark' (with 10 species suggested for conservation breeding each indicated by an asterisk) (http://portal.isis.org/partners/AARK/Lists/Prioritization%20workshop%20results/AllItems.aspx; accessed 5 July 2010). Species are sorted by risk factor; in 48 taxa the biotic index and risk factor were not determined

Species	IUCN Red List category	Geographic range (km^2)	Biotic index (Bielby et al. 2008)	Risk factor (Rödder et al. 2009)	'Amphibian Ark' priority value
Aglyptodactylus laticeps	EN	31.9	0.8	0	44
Boophis jaegeri	VU	413.95	0.36	0	12
Boophis xerophilus	DD	195.58	0.35	0	8
Heterixalus tricolor	LC	28.15	0.99	0	0
Heterixalus variabilis	LC	3356.71	0.22	0	0
Mantidactylus cowanii	NT	34854.52	0.18	0	0
Mantidactylus melanopleura	LC	99953.85	0.3	0	8
Mantidactylus noralottae	VU	3.62	0.35	0	0
Rhombophryne testudo	VU	570.4	0.51	0	15
Stumpffia psologlossa	DD	1919.09	0.58	0	8
Stumpffia pygmaea	VU	328.57	0.46	0	20
Heterixalus luteostriatus	LC	49184.02	0.1	0	0
Aglyptodactylus securifer	LC	6372.37	0.27	0	11
Wakea madinika	DD	93.47	1	0	11
Hoplobatrachus tigerinus	LC	4202408.01	0.05	0	5
Dyscophus insularis	LC	152722.46	0.09	0	3
Scaphiophryne calcarata	LC	165446.88	0.09	0	3
Mantella betsileo	LC	89439.46	0.15	0	10
Blommersia wittei	LC	74120.37	0.11	0	0
Boophis doulioti	LC	279388.71	0.12	0	0
Scaphiophryne brevis	LC	90888.33	0.16	0	3
Ptychadena mascareniensis	LC	9151425.38	0.06	0.01	0

(continued)

Table 14.1 (continued)

Species	IUCN Red List category	Geographic range (km^2)	Biotic index (Bielby et al. 2008)	Risk factor (Rödder et al. 2009)	'Amphibian Ark' priority value
Heterixalus carbonei	NT	4858	0.28	0.01	4
Heterixalus boettgeri	LC	4938.35	0.25	0.01	0
Mantella viridis	EN	839	1	0.01	47*
Boophis opisthodon	LC	49586.7	0.12	0.03	0
Cophyla phyllodactyla	LC	10255.36	0.43	0.06	3
Gephyromantis luteus	LC	72241.32	0.17	0.07	0
Stumpffia gimmeli	LC	9512.22	0.5	0.07	0
Mantidactylus zipperi	LC	76195.45	0.51	0.08	0
Mantidactylus ulcerosus	LC	54277.51	0.63	0.1	0
Heterixalus punctatus	LC	36614.74	0.28	0.13	0
Mantidactylus ambreensis	LC	8198.09	0.61	0.13	0
Boophis tephraeomystax	LC	123576.94	0.23	0.14	0
Mantidactylus curtus	LC	254685.51	0.27	0.14	8
Stumpffia tetradactyla	DD	495.35	0.54	0.14	16
Scaphiophryne spinosa	LC	103192.65	0.23	0.14	13
Mantella expectata	EN	1290.53	1	0.15	47*
Mantella laevigata	NT	23090.51	0.33	0.15	22
Boophis haematopus	VU	4109.44	0.44	0.15	12
Platypelis grandis	LC	145481.81	0.25	0.17	8
Heterixalus alboguttatus	LC	35515.74	0.26	0.17	0
Mantella manery	DD	37.13	0.93	0.17	18
Mantidactylus majori	LC	40087.57	0.98	0.18	0
Gephyromantis plicifer	NT	20275.76	0.3	0.18	4
Gephyromantis boulengeri	LC	30019.63	0.33	0.19	0
Scaphiophryne gottlebei	EN	724.96	1	0.19	60*
Plethodontohyla ocellata	LC	78481.67	0.28	0.19	0
Mantidactylus femoralis	LC	210805	0.29	0.21	0

Gephyromantis malagasius	LC	69119.48	0.3	0.22	0
Gephyromantis redimitus	LC	55563.98	0.3	0.22	0
Mantidactylus betsileanus	LC	96904.14	0.3	0.24	8
Guibemantis liber	LC	159146	0.31	0.25	0
Gephyromantis corvus	EN	1239.26	0.76	0.25	13
Mantidactylus lugubris	LC	115484.08	0.36	0.26	0
Gephyromantis silvanus	EN	892.25	0.7	0.27	44
Gephyromantis pseudoasper	LC	22586.44	0.51	0.27	0
Mantidactylus guttulatus	LC	60561.53	0.37	0.27	13
Platypelis milloti	EN	3529.49	0.83	0.28	44
Platypelis pollicaris	DD	12442.21	0.57	0.29	8
Gephyromantis webbi	EN	1649.04	0.64	0.29	36
Mantidactylus biporus	LC	96111.76	0.35	0.29	0
Platypelis barbouri	LC	41782.08	0.4	0.3	0
Guibemantis tornieri	LC	69844.24	0.34	0.31	0
Stumpffia grandis	DD	25270.95	0.43	0.31	8
Mantidactylus opiparis	LC	82533.99	0.41	0.31	0
Mantidactylus mocquardi	LC	139555.73	0.35	0.31	0
Mantella nigricans	LC	31432.53	0.45	0.31	10
Boophis albilabris	LC	90431.13	0.36	0.32	0
Mantidactylus grandidieri	LC	85656.99	0.29	0.32	13
Gephyromantis granulatus	LC	15283.02	0.57	0.32	0
Gephyromantis zavona	DD	745.06	0.98	0.32	8
Boophis tasymena	LC	69295.9	0.37	0.32	0
Boophis occidentalis	NT	652.75	0.9	0.33	4
Guibemantis pulcher	LC	67174.54	0.36	0.33	0
Gephyromantis horridus	EN	3243.21	0.85	0.33	44
Blommersia grandisonae	LC	68237.09	0.37	0.34	0
Boophis madagascariensis	LC	99482.06	0.38	0.34	8
Paradoxophyla palmata	LC	35398.42	0.42	0.34	11

(continued)

Table 14.1 (continued)

Species	IUCN Red List category	Geographic range (km^2)	Biotic index (Bielby et al. 2008)	Risk factor (Rödder et al. 2009)	'Amphibian Ark' priority value
Gephyromantis moseri	LC	32336.51	0.42	0.34	0
Spinomantis aglavei	LC	100698.02	0.38	0.34	0
Boophis hillenii	DD	15039.61	0.53	0.35	8
Heterixalus betsileo	LC	119509.18	0.4	0.35	0
Boophis albipunctatus	LC	38429.16	0.42	0.36	0
Gephyromantis rivicola	VU	9008.09	0.54	0.36	12
Boophis boehmei	LC	69297.28	0.39	0.36	0
Spinomantis peraccae	LC	112472.12	0.39	0.37	0
Boophis viridis	LC	67939.83	0.39	0.37	0
Boophis pauliani	LC	52880.96	0.42	0.37	0*
Boophis andreonei	VU	1426.18	0.92	0.38	12
Boophis reticulatus	LC	67718.81	0.42	0.38	8
Mantidactylus tricinctus	DD	2625.07	1	0.38	8
Heterixalus andrakata	LC	1136.93	0.76	0.38	0
Guibemantis punctatus	DD	11984.08	0.55	0.38	8
Dyscophus antongilii	NT	5264.81	0.57	0.39	12
Boophis brachychir	DD	6523.13	0.65	0.39	8
Gephyromantis asper	LC	45983.06	0.45	0.4	0
Boophis goudotii	LC	91462.49	0.45	0.4	0
Mantella madagascariensis	VU	13914.61	0.44	0.4	22
Spinomantis fimbriatus	LC	38131.65	0.47	0.41	0
Boophis miniatus	LC	31016.03	0.47	0.42	0
Gephyromantis spinifer	NT	28829.74	0.52	0.44	4
Dyscophus guineti	LC	7135.13	0.64	0.44	8
Mantidactylus aerumnalis	LC	42295.77	0.46	0.45	0
Gephyromantis decaryi	NT	18617.09	0.5	0.45	4
Mantella pulchra	VU	17751.99	0.55	0.46	22

Stumpffia tridactyla	DD	1213.56	0.84	0.46	8
Spinomantis bertini	NT	25632.84	0.5	0.46	4
Boophis idae	LC	37094.62	0.47	0.46	0
Boophis rappiodes	LC	36815.13	0.47	0.46	0
Boophis marojezensis	LC	46017.99	0.48	0.46	0
Mantidactylus zipperi	LC	48425.56	0.28	0.47	0
Boophis pyrrhus	LC	33584.44	0.52	0.47	0
Boophis luteus	LC	42584.25	0.5	0.48	8
Boophis picturatus	LC	32307.51	0.48	0.48	0
Platypelis tetra	EN	6756.66	0.63	0.49	44
Mantidactylus argenteus	LC	31887.43	0.51	0.5	0
Mantella baroni	LC	37510.05	0.51	0.51	10
Boophis vittatus	LC	12464.45	0.66	0.51	0
Gephyromantis striatus	VU	4886.48	0.67	0.52	12
Spinomantis elegans	VU	20489.63	0.55	0.52	12
Blommersia domerguei	LC	58378.34	0.53	0.52	0
Boophis guibei	LC	22625.61	0.52	0.52	0
Gephyromantis tandroka	VU	10762.58	0.68	0.53	12
Heterixalus rutenbergi	NT	52372.63	0.6	0.53	4
Plethodontohyla mihanika	LC	37795.36	0.57	0.54	8
Mantella haraldmeieri	VU	2385.73	0.8	0.56	22
Boophis bottae	LC	19258.93	0.57	0.57	0
Guibemantis albolineatus	DD	11994.87	0.68	0.57	8
Gephyromantis blanci	NT	21342.83	0.6	0.58	4
Blommersia blommersae	LC	20046.08	0.6	0.6	0
Gephyromantis salegy	VU	2411.23	0.78	0.61	12
Boophis erythrodactylus	LC	18211.35	0.66	0.62	0
Boophis rhodoscelis	NT	22207.75	0.66	0.62	12
Boophis blommersae	VU	1857.27	0.95	0.63	12
Boophis microtympanum	LC	34738.96	0.63	0.63	0

(continued)

Table 14.1 (continued)

Species	IUCN Red List category	Geographic range (km^2)	Biotic index (Bielby et al. 2008)	Risk factor (Rödder et al. 2009)	'Amphibian Ark' priority value
Scaphiophryne marmorata	VU	13186.32	0.64	0.64	25
Boophis majori	NT	19767.4	0.65	0.65	4
Boophis ankaratra	LC	35360.77	0.66	0.65	0
Gephyromantis ambohitra	VU	1244.13	0.97	0.65	12
Boophis rufioculis	NT	17871.18	0.65	0.65	4
Mantidactylus alutus	LC	38272.38	0.65	0.65	0
Anodonthyla nigrigularis	DD	2268.21	0.87	0.68	11
Gephyromantis klemmeri	VU	3351.33	0.84	0.68	12
Spinomantis guibei	EN	5984.76	0.8	0.7	44
Boophis englaenderi	DD	636.04	0.95	0.72	8
Gephyromantis cornutus	DD	10700.35	0.77	0.75	8
Mantella cowanii	CR	287.38	0.76	0.76	51*
Spinomantis brunae	EN	1488.94	0.86	0.78	44
Boophis elenae	DD	5154.56	0.78	0.78	8
Blommersia sarotra	DD	6765.31	0.8	0.8	8
Madecassophryne truebae	EN	4366.38	0.83	0.82	44
Gephyromantis tschenki	DD	4583.14	0.83	0.83	8
Blommersia kely	LC	10432.06	0.86	0.86	0
Gephyromantis eiselti	DD	2225.89	0.91	0.91	8
Gephyromantis enki	DD	1486.97	0.93	0.93	8
Boophis periegetes	DD	1339.56	0.94	0.94	8
Plethodontohyla brevipes	EN	580.73	0.95	0.95	44
Plethodontohyla tuberata	VU	3895.6	0.96	0.96	20
Boophis laurenti	DD	1076.87	0.96	0.96	8
Boophis liami	DD	1181.38	0.96	0.96	8
Gephyromantis thelenae	DD	951.19	0.96	0.96	8
Boophis schuboeae	DD	563.94	0.97	0.97	8

Boophis anjanaharibeensis	DD	373.27	0.98	0.98	8
Mantidactylus madecassus	EN	1431.53	0.32	0.98	44
Boophis solomaso	DD	793.19	0.98	0.98	8
Platypelis alticola	EN	1035.38	0.99	0.98	44
Boophis sibilans	DD	697.25	0.98	0.98	16
Platypelis mavomavo	EN	531.66	0.98	0.98	44
Boophis andohahela	DD	345.61	0.99	0.98	8
Mantella aurantiaca	CR	601.34	0.99	0.99	51*
Spinomantis microtis	EN	430.89	0.99	0.99	44
Guibemantis kathrinae	DD	491.74	0.99	0.99	8
Boophis feonnyala	DD	360.83	0.99	0.99	8
Anodonthyla montana	VU	644.86	1	1	15
Anodonthyla rouxae	EN	124.06	1	1	47
Boophis burgeri	DD	163.84	1	1	8
Boophis mandraka	DD	260.07	1	1	8
Boophis williamsi	CR	407.99	1	1	56*
Gephyromantis schilfi	VU	27.03	1	1	12
Mantella crocea	EN	259.96	1	1	26
Mantella milotympanum	CR	56.19	1	1	46*
Mantidactylus pauliani	CR	286.38	0.41	1	56*
Mantidactylus zolitschka	DD	311.83	1	1	8
Scaphiophryne boribory	EN	401.65	1	1	29
Stumpffia helenae	CR	322.78	1	1	46*
Mantidactylus delormei	VU	2287.11	not dermined	not dermined	0
Spinomantis massi	VU	10054.3	not dermined	not dermined	12
Spinomantis phantasticus	LC	33914.54	not dermined	not dermined	0
Aglyptodactylus madagascariensis	LC	170824.75	not dermined	not dermined	8
Anodonthyla moramora	DD	12.19	not dermined	not dermined	11
Boehmantis microtympanum	EN	5701.03	not dermined	not dermined	52
Boophis axelmeyeri	NT	375.46	not dermined	not dermined	no data

(continued)

Table 14.1 (continued)

Species	IUCN Red List category	Geographic range (km^2)	Biotic index (Bielby et al. 2008)	Risk factor (Rödder et al. 2009)	'Amphibian Ark' priority value
Boophis lichenoides	LC	64929.79	not dermined	not dermined	0
Boophis sambirano	VU	1275.25	not dermined	not dermined	8
Boophis septentrionalis	DD	1275.12	not dermined	not dermined	8
Boophis tampoka	EN	47.81	not dermined	not dermined	0
Cophyla berara	CR	10.24	not dermined	not dermined	11
Cophyla occultans	DD	3264.5	not dermined	not dermined	8
Gephyromantis azzurrae	EN	9.1	not dermined	not dermined	0
Gephyromantis leucocephalus	NT	12978.4	not dermined	not dermined	4
Gephyromantis leucomaculatus	NT	20951.6	not dermined	not dermined	4
Gephyromantis runewsweeki	EN	29.08	not dermined	not dermined	no data
Gephyromantis sculpturatus	LC	16525.55	not dermined	not dermined	0
Gephyromantis ventrimaculatus	LC	37318.97	not dermined	not dermined	0
Guibemantis bicalcaratus	LC	130407.16	not dermined	not dermined	0
Guibemantis depressiceps	LC	152182	not dermined	not dermined	0
Guibemantis flavobrunneus	LC	70833.65	not dermined	not dermined	0
Guibemantis timidus	LC	28279.98	not dermined	not dermined	0
Heterixalus madagascariensis	LC	33716.12	not dermined	not dermined	0
Laliostoma labrosum	LC	338436.67	not dermined	not dermined	3
Mantella bernhardi	EN	13903.13	not dermined	not dermined	42*
Mantella ebenaui	LC	46818.91	not dermined	not dermined	10
Mantidactylus albofrenatus	DD	2070.17	not dermined	not dermined	8
Mantidactylus ambohimitombi	DD	295.14	not dermined	not dermined	8
Mantidactylus bellyi	LC	14334.86	not dermined	not dermined	no data
Mantidactylus bourgati	DD	1512.35	not dermined	not dermined	0
Mantidactylus brevipalmatus	LC	43516.61	not dermined	not dermined	0
Paradoxophyla tiarano	DD	9.89	not dermined	not dermined	11
Platypelis cowanii	DD	no data	not dermined	not dermined	8

Platypelis tsaratananaensis	VU	25.52	not dermined	not dermined	12
Platypelis tuberifera	LC	66461.9	not dermined	not dermined	0
Plethodontohyla angulifera	DD	no data	not dermined	not dermined	8
Plethodontohyla bipunctata	LC	52478.29	not dermined	not dermined	0
Plethodontohyla fonetana	VU	16.89	not dermined	not dermined	0
Plethodontohyla guentheri	DD	3.34	not dermined	not dermined	8
Plethodontohyla inguinalis	LC	80354.97	not dermined	not dermined	0
Plethodontohyla notosticta	LC	903.56	not dermined	not dermined	8
Scaphiophryne madagascariensis	NT	23694.27	not dermined	not dermined	7
Scaphiophryne menabensis	NT	31618.63	not dermined	not dermined	11
Scaphiophryne obscura	DD	no data	not dermined	not dermined	11
Scaphiophryne verrucosa	DD	16.63	not dermined	not dermined	11
Stumpffia roseifemoralis	DD	1367.67	not dermined	not dermined	8
Tsingymantis antitra	VU	11.52	not dermined	not dermined	8

14.2 Amphibian Hotspot Madagascar: A Special Case

14.2.1 Anuran Megadiversity

The amphibian fauna of Madagascar is highly exceptional both in terms of species diversity and endemism and is represented only by frogs (order Anura), whereas the two other orders (Caudata and Gymnophiona) are absent. With currently more than 270 described species and probably more than 200 still undescribed species (Vieites et al. 2009), Madagascar has the highest amphibian species diversity of all African countries and clearly ranks among the global amphibian hotspots. Diversity is concentrated in rainforests along the East coast mainly between sea level and 1,000 m above sea level and can locally reach over 100 species (Andreone et al. 2008), whereas the largely deforested central high plateau and the relatively dry western slopes harbor much fewer species (Glaw and Vences 2007). Impressively, 100% of the autochthonous species and 88% of the genera are naturally endemic to Madagascar and its inshore islands. Recent studies indicate that the degree of microendemism is much higher than formerly expected (e.g., Gehring et al. 2011), indicating that the currently recognized geographic range size of many species (Table 14.1) might be an overestimate that will strongly decrease when taxonomic progress (e.g., by increasing use of integrative taxonomy) will have deciphered the relationships within all species complexes. Furthermore, the continuing high level of deforestation and fragmentation of primary forests will result in a further decrease of available habitats, population size, and density (Vallan 2000). All these factors increase the potential impact that can be expected from an outbreak of chytridiomycosis on this “micro-continent”.

14.2.2 Potential Impact of Chytridiomycosis

Bd has so far not been detected in Madagascar despite reasonably thorough survey activities. At least, eight localities have been surveyed covering the three major biogeographical regions and a wide range of altitudes with more than 500 samples from 74 different species (Weldon et al. 2008). This implies that the pathogen may currently be absent on the island.

How likely is *Bd* to enter Madagascar? The dispersal ability of this pathogen is indisputably high, even though mechanism and pathways are areas of ongoing debate and discovery (e.g., Fisher et al. 2009). Temporal patterns of spread have been studied in the Neotropics and show a possible annual range expansion of 25–282 km where the lower end of the spectrum is more prominent in well-studied areas (Lips et al. 2008). Importantly, the island status of Madagascar does not exclude the possibility of *Bd* invasion. There have been reports of *Bd* emergence on more than 20 islands all over the World including remote oceanic systems like Hawaii (http://www.spatialepidemiology.net/Bd-maps). This underlines the imminent danger that *Bd* may enter Madagascar. Because of the remoteness of this island, human-mediated spread may be the most likely pathway of introduction (Wollenberg et al. 2010). Possible modes of import include infected live or dead amphibians, fishes or contaminated water, moist substrates, or other fomites (i.e., via animal trade or accidental cointroduction with other imported products). Interestingly, on the African mainland, *Bd* has been detected widespread with high prevalence (Kielgast et al. 2010) and may hence potentially serve as a source of introduction.

Rödder et al. (2009), in their ecological niche model, identified a major portion of Madagascar to be highly climate-suitable to the chytrid fungus. When comparing the areas within the island that are most suitable to the fungus with amphibian species richness, a remarkable spatial impact is evident (Fig. 14.1). When applying

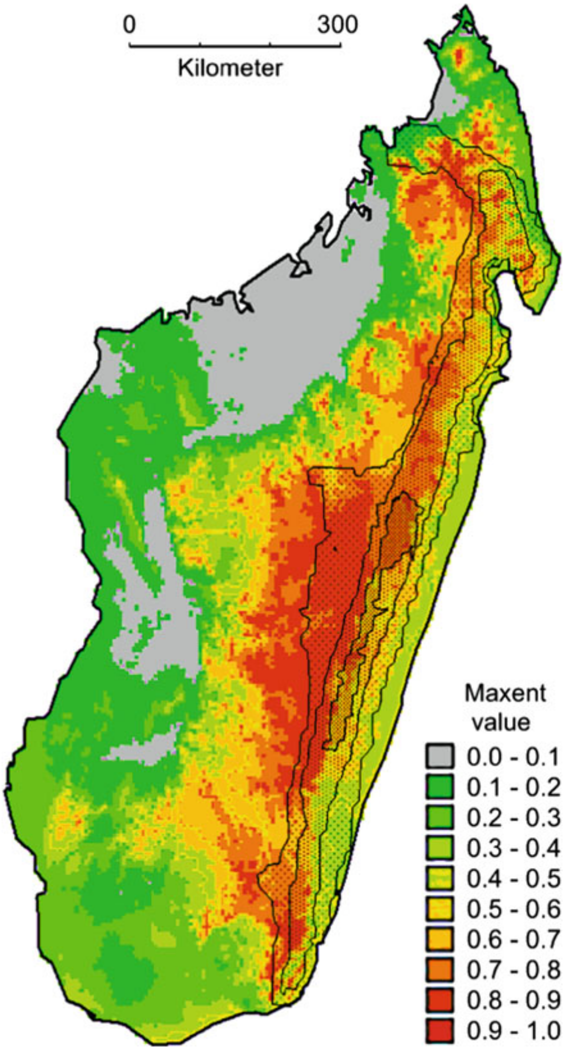

Fig. 14.1 Potential distribution of the amphibian chytrid fungus in Madagascar following the risk assessment of Rödder et al. (2009), re-projected from a resolution of 2.5 arc min to 30 arc sec. In this ecological niche model, warmer colors indicate a higher climatic suitability. Amphibian species richness as proposed by Kremen et al. (2008) is highlighted from lighter to darker stippling: >18, >36, >63 species per grid cell of 0.1°

the rule set of predictions from the ecological niche and key host life history traits (Rödder et al. 2009), 40 of 186 considered Madagascan anurans (i.e. 234 recorded species less 48 for which no biotic index is available) exhibit risk factor 0.75 or higher (Table 14.1), including many species with small ranges from higher altitudes. We expect that the inclusion and exclusion of species has to be taken with care in some cases, as the risk factor of Rödder et al. (2009) highly depends on the geographic range encompassed by a species. If this is remarkably small, this may merely reflect limited collections efforts in remote areas. If a species' distribution is extraordinarily large, this can be the result of an unsolved taxonomy. However, with the current state of knowledge, it remains unanswered if emergence of chytridiomycosis on Madagascar will in fact lead to amphibian decline or extinctions. The only available empirical evidence of susceptibility comes from an outbreak in captive Tomato Frogs (*Dyscophus antongilii*) with high mortality rate (Oevermann et al. 2005) and, more recently, infection of captive *Plethodontohyla tuberata* (Une et al. 2008). Due to the long history of evolutionary isolation it may be expected that Madagascan amphibians naïve to *Bd* will respond with drastic population declines.

Comparing the potential risk imposed by *Bd* with the prioritization for Madagascan amphibians as proposed by the "Amphibian Ark", there is little overlap (Fig. 14.2, Table 14.1). Particularly noteworthy is that "Amphibian Ark"

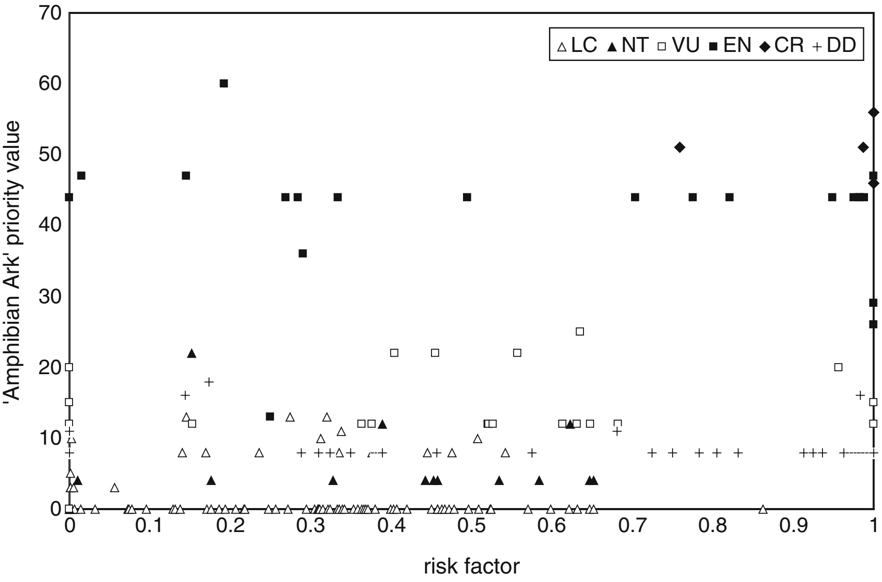

Fig. 14.2 Relationship between IUCN Red List status, conservation priorities according to "Amphibian Ark" and corresponding risk factor, indicating threat of extinction by the emergence of chytridiomycosis, as proposed by Rödder et al. (2009). Data are taken from Table 14.1. IUCN Red List categories are: *DD* Data Deficient, *LC* Least Concern, *NT* Near Threatened, *VU* Vulnerable, *EN* Endangered, *CR* Critically Endangered (http://www.redlist.org)

prioritized only 10 out of 242 species assessed for ex situ conservation measures. As indicated in Table 14.1, five of these are potentially exposed to a high risk of extinction through *Bd* following Rödder et al. (2009), while for one (*Mantella bernhardi*) no risk factor was assessed. The four remaining are expected to be little affected by potential *Bd* introduction (Table 14.1).

In conclusion, Madagascar's unique and rich amphibian diversity may be expected to potentially suffer heavy consequences post *Bd* introduction and running ex situ conservation measures may not be sufficient to cushion the threat.

14.2.3 Recommendations for Conservation Strategies

Even though the Madagascan species prioritized by "Amphibian Ark" represent a minute fraction of the island's amphibian diversity at stake, the proportion of Madagascan species that are considered for conservation breeding, compared to other regions, e.g., African mainland, is considerably high (Lötters 2008). This illustrates a strong recognition of the importance of the distinctive Madagascan amphibian fauna (e.g., Andreone et al. 2008). Therefore, species prioritization by "Amphibian Ark", in principle, has to be seen as a first step forward. In a subsequent step, we recommend a revision of the 'Amphibian Ark' prioritization considering the particular threat to species through chytridiomycosis (e.g., risk factor of Rödder et al. 2009). Furthermore, additional short-term conservation breeding programs should be implemented in advance to develop breeding procedures and conditions for representatives of all major clades of Madagascan amphibians and representatives of the different reproductive modes (Buley et al. 2008). These "breeding manuals," which might be obtained in close cooperation with qualified hobbyist breeders, would allow to establish captive breeding programs without delay in the expected case of *Bd*'s arrival in Madagascar. This preemergency prophylaxis might be a crucial measure, as *Bd* spread and population breakdowns may undergo within a couple of months only after *Bd* arrival (e.g., Lips et al. 2008), and it remains uncertain which species or taxonomic groups will be most heavily affected. For the same reason, following the interventions advocated through the IUCN Amphibian Conservation Action Plan (Gascon et al. 2007), there is a strong need to develop plans for "emergency response". That is collecting, treating, quarantining, and subsequently using for breeding efforts as many as possible specimens per species and perhaps as many as possible localities where populations are observed to decline due to chytridiomycosis (Gascon et al. 2007). This may especially aim on the provision of funding and ex situ capacities and ad hoc coordination, permission, and transport facilitation. This may give reason to consider the establishment of an in-country conservation breeding center. Noteworthy, emergency response can only be effectively established when species are monitored, i.e., both population and *Bd* status.

As a preventive and certainly the "best" measure, we here stress the need for an increased attention to "biosecurity." The implementation of quarantine measures related to commercial trade in aquarium fishes and plants to prevent the accidental introduction of the amphibian chytrid fungus into Madagascar is in progress (Andreone et al. 2008). However, a more rigorous import risk assessment is still needed to create a basis for further strategies and possibly specific restrictions to mitigate the threat posed by *Bd* to Madagascar's megadiverse anuran fauna.

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Part IV
Biodiversity in the Tropics

Chapter 15
Impacts of Biofuel Expansion in Biodiversity Hotspots

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Abstract The finitude of fossil fuels, concerns for energy security, and the need to respond to climate change has led to growing worldwide interests in biofuels. However, a significant proportion of conventional biofuel feedstocks is produced in the tropics, notably oil palm in Southeast Asia, and soy and sugarcane in Brazil. This is a worrying trend for many tropical biologists, because it is also within the tropics where the majority of the world's biodiversity hotspots are located (Myers et al. 2000). For at least the next decade, first generation biofuels will still be in demand. In biodiversity hotspots, where a myriad of anthropogenic factors are already driving intense land use conflicts, biofuel production will pose an additional challenge to the preservation of the remaining natural habitats. Here we address the following questions: How does biofuel expansion threaten biodiversity hotspots? How can we reconcile biofuel expansion with biodiversity conservation in these hotspots?

15.1 Biofuels in Biodiversity Hotspots

Approximately 80% of total world energy supply is derived from fossil fuels such as oil, natural gas, and coal. Fossil fuels are finite sources of energy and are estimated to last anywhere from 41 to ~700 years, depending on production and consumption rates (Goldemberg and Johansson 2004; Goldemberg 2007). Growing demand for energy from industrialized nations, such as the United States, as well as emerging economies, such as China and India, will continue to place tremendous pressures on world petroleum supplies in the next few decades (Worldwatch Institute 2007). This trend is reflected in the price of crude oil, which has risen

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from ~US$25 per barrel in January 2000 to ~US$76 per barrel in January 2010 (peaking at ~US$140 per barrel in June 2008) (EIA-DOE 2010). As such, many countries are seeking to diversify their energy portfolio. Growing concerns over anthropogenic climate change have also driven countries to search for alternatives to fossil fuels that can help lower greenhouse gas emissions and slow the pace of global warming (Koh and Ghazoul 2008).

These pressing global energy and environmental challenges have at least partly driven the recent worldwide interest in biofuels. Both developed (e.g., the United States) and developing nations (e.g., China) view biofuels as a renewable energy source that can help achieve energy security, decrease greenhouse gas emissions, and fulfill rural development standards (Fulton et al. 2004, Armbruster and Coyle 2006; Pickett et al. 2008; Koh et al. 2008; Rist et al. 2009). Between 1980 and 2005, global biofuel production increased from 4.4 to 50.1 billion liters (Murray 2005, Armbruster and Coyle 2006). Recently, several of these countries have also announced ambitious targets for switching from fossil fuels to renewable fuels (Worldwatch Institute 2007).

Biofuels are renewable fuels derived from biological feedstocks. Currently, the most widely used liquid biofuels in the transportation sector are bioethanol and biodiesel. Bioethanol is produced from the fermentation of corn (*Zea mays*), sugarcane (*Saccharum spp.*), or other starch- or sugar-rich crops. Biodiesel is manufactured from vegetable oil (e.g., soybean (*Glycine max* L.), oil palm (*Elaeis guineensis*) or animal fats. At present, bioethanol is primarily produced from corn in the United States, and from sugarcane in Brazil. Biodiesel is produced largely from rapeseed and sunflower seed oil in Europe, and soybean oil in the United States. However, there is a steadily growing demand for palm oil produced in the tropics due to its much higher yield (~5,000 l per ha compared to ~1,200 l per ha for rapeseed), and hence lower production costs (Worldwatch Institute 2007). This is a worrying trend for many tropical biologists, because it is also within the tropics where the majority of the world's biodiversity hotspots are located (Conservation International 2010; http://www.biodiversityhotspots.org). Furthermore, high proportions of yet forested lands in these hotspots may be suitable for biofuel production (Table 15.1). A recent study estimated that an increase in global biodiesel production capacity to meet future biodiesel demands (an estimated 277 million tons per year by 2050) may lead to potential habitat losses of between 0.4 million and 114.2 million ha within these hotspots, depending on the feedstock (Koh 2007). Without proper mitigation guidelines, the future expansion of biodiesel feedstock production in biodiversity hotspots will likely threaten their native biodiversity (Mittermeier et al. 2004; Koh and Ghazoul 2008).

Some researchers argue that "next generation" biofuels, produced from nonfood feedstocks such as agricultural wastes, can fulfill many of the promises of renewable fuels without much of the environmental ills (Shi et al. 2009). These second and third generation biofuels are currently too costly to be produced on a commercial scale. Nevertheless, they may become more readily available and affordable in the future through technological breakthroughs, driven by strong governmental

Table 15.1 Total forested area suitable for biofuel feedstock in 14 tropical hotspots

		Total forested area suitable for biofuel feedstock crops[b]					
Biodiversity hotspot regions	Total forested area (1,000 ha)[a]	Oil Palm		Sugarcane		Soybean	
		1,000 ha	%[c]	1,000 ha	%[c]	1,000 ha	%[c]
Latin America							
Mesoamerica	62,546	7,570	12.1	16,821	26.9	8,808	14.1
Atlantic Forest	25,595	3,544	13.8	7,754	30.3	3,303	12.9
Cerrado[d]	88,701[d]	2,182	2.5	10,052	11.3	16,717	18.8
Tropical Andes	45,175	3,404	7.5	3,076	6.8	3,271	7.2
Tumbes-Choco-Magdalena	8,371	3,505	41.9	1,541	18.4	137	1.6
Africa							
Guinean Forests of West Africa	22,854	4,162	18.2	6,015	26.3	954	4.2
Coastal Forests of Eastern Africa	20,087	7	0.04	2,661	13.2	11,284	56.2
Madagascar and the Indian Ocean Islands	13,483	858	6.4	1,762	13.1	2,765	20.5
Asia							
Western Ghats and Sri Lanka	10,402	324	3.1	660	6.3	2,385	22.9
Indo-Burma	79,931	637	0.8	4,511	5.6	2,124	2.7
Philippines	8,419	834	9.91	533	6.3	26	0.3
Sundaland	77,674	25,729	33.1	10,098	13.0	49	0.1
Wallacea	19,823	2,348	11.8	1,014	5.1	101	0.5
East Melanesian Islands	7,762	1,011	13.0	170	2.1	0	0.0

[a] Total forested area was calculated using the global land cover 2000 database (European Commission 2003) by aggregating all land cover classes with an open or closed tree canopy cover (classes 1–9 from the global legend,) and therefore includes secondary and primary forest formations with a tree cover higher than 15%

[b] Suitability maps for each of the crops were obtained from the Global Agro-ecological Assessment (Fischer et al. 2002) by aggregating the moderate, medium, good, high and very high suitability categories for each of the crops. Thus, the suitable area presented for each of the hotspots encompasses any forested area (or shrubland in the case of the Cerrado hotspot) with an attainable yield higher than the 25% of the global maximum potential yield. This area is also presented as a percentage
(c) of the total forested area[a]

[d] Calculations for the Cerrado hotspot were based on the South America regional dataset from the global land cover 2000 project (Eva et al. 2002; European Commission 2003) in order to include not only forested areas but also Shrub Savannahs and Open/Close Shrublands (regional classes 61, 64 and 65), which are dominant and highly diverse natural ecosystems in this hotspot

support and a string of local government and international subsidies and initiatives (Doornbosch and Steenblik 2007). Even so, next generation biofuels may not be completely free of environmental trade-offs. A recent study that analyzed the potential environmental impacts of a global, aggressive cellulosic biofuels program, projected major losses for biodiversity within biodiversity hotspots both directly, by replacing native habitats, or indirectly, by displacing other agricultural land uses onto native habitats (Melillo et al. 2009).

For at least the next decade, first generation biofuels will still be in demand (OECD-FAO 2008). In biodiversity hotspots, where a myriad of anthropogenic factors are already driving intense land use conflicts, adding biofuels as another demand on the land will make the preservation of the remaining natural habitats an even greater challenge. Hence, it is imperative for us to assess the impacts of biofuel expansion on biodiversity hotspots by asking the following two questions: (1) How does biofuel expansion threaten biodiversity within biodiversity hotspots? (2) How might we reconcile biofuel expansion with biodiversity conservation in these hotspots?

15.2 How Does Biofuel Expansion Threaten Biodiversity Within Biodiversity Hotspots?

15.2.1 Habitat Loss

Currently, biodiversity hotspots in Southeast Asia and Latin America are under the greatest threat of biofuel expansion, namely from oil palm, sugarcane, and soybean expansion (Koh and Wilcove 2007, 2008, 2009; Wilcove and Koh 2010). Based on land-cover data compiled by the Food and Agriculture Organization of the United Nations, Koh and Wilcove (2008) calculated an expansion of 1.8 million ha of oil palm in Malaysia and three million ha in Indonesia between 1995 and 2005. Approximately 55–59% of this oil palm expansion in Malaysia and at least 56% of that in Indonesia occurred at the expense of primary or logged over forests. In Brazil, the area of soybean expansion increased dramatically by 10 million ha, from 11.6 million to 22.9 million ha between 1995 and 2005 (FAO 2010). Successful expansion of soybean has been driven by a biotechnological breakthrough–the development of soybean–bacteria combinations with pseudosymbiotic relationships, which allows soybeans to be planted with little or no application of nitrogen fertilizers (Fearnside 2001). Although much of this soybean expansion has occurred on nonforested lands, particularly in the Cerrado, this natural ecosystem nonetheless contains high concentrations of endemic and threatened species and has been delineated as a biodiversity hotspot (Fearnside 2001). Sugarcane expansion in Brazil has almost doubled from 4.5 million ha in 1995 to 8.1 million ha in 2008, with a rapid increase of 2.3 million ha between 2005 and 2008 (FAO 2010). Even though sugarcane plantings so far have mostly replaced pasture lands, continued expansion of sugarcane-bioethanol into Central Brazil will likely displace cattle ranchers and soybean producers onto the Amazon and Atlantic Forest and lead to extensive deforestation (Martinelli and Filoso 2008; Lapola et al. 2010). The expansion of biofuel industries is not the only cause of habitat loss in these areas; other causes include large-scale commercial logging, pulp and paper industries, cattle ranching, shifting cultivation, mining, urban development, and agricultural expansion of other crops (Angelsen and Kaimowitz 1999). However, growing global demand for palm oil, soybean, and sugarcane for biofuels will likely exacerbate deforestation in these hotspots over the next decade (IATP 2008).

15.2.2 Biodiversity Loss

Conversion of natural habitats into monocultures, by definition, implies a drastic loss in biodiversity and change in the composition of species communities in the area. Oil palm plantations contain less than half as many vertebrate species as primary forests (Fitzherbert et al. 2008). Forest bird species declined by 73–77% (Koh and Wilcove 2008) and only 10% of mammal species were detected in oil palm plantations (Maddox et al. 2007). Endangered species such as the Sumatran tiger (*Panthera tigris sumatrae*), tapirs (*Tapirus indicus*), and clouded leopards (*Neofelis nebulosa*) were never recorded in oil palm plantations; and most mammals even preferred marginal and heavily degraded landscapes, such as shrublands, to oil palm (Maddox et al. 2007). Mammals that do occur in oil palm plantations tend to be of low conservation value, and are dominated by a few generalist species such as the wild pig (*Sus scrofa*), bearded pig (*Sus barbatus*), leopard cat (*Prionailurus bengalensis*), and common palm civet (*Paradoxurus hermaphroditus*) (Maddox et al. 2007). Invertebrate taxa showed greater variation between oil palm plantations and natural forests (Fitzherbert et al. 2008). For example, the conversion of forests to oil palm caused forest butterfly species to decline by 79–83% (Koh and Wilcove 2008); whereas ants, moths, and bees showed a higher total species richness in oil palm plantations than forests (Danielsen et al. 2009). Nevertheless, studies consistently showed a dominance of nonforest invertebrate species in oil palm plantations (Danielsen et al. 2009). Comparing across both vertebrate and invertebrate taxa, a mean of only 15% of species recorded in primary forest could be found in oil palm plantations (Fitzherbert et al. 2008). Not surprisingly, plant diversity within oil palm plantations was impoverished compared to forests due to regular maintenance and replanting (every 25–30 years) of oil palm fields (Fitzherbert et al. 2008; Danielsen et al. 2009). Biodiversity loss from soybean and sugarcane production has not been as well studied as oil palm but is expected to be substantial by virtue of large scale natural habitat conversion (Fearnside 2001).

The Cerrado is the largest savanna region in South America and contains a rich diversity of different vegetation types, from tree and scrub savanna, grasslands with scattered trees, and patches of dry, closed-canopy forests known as the Cerradão (Conservation International 2010). This region contains a large number of plant (10,000 species) and animal species (2,000 vertebrate species), including many endemic species such as the maned wolf (*Chrysocyon brachyurus*), the giant armadillo (*Priodontes maximus*), and the giant anteater (*Myrmecophaga tridactyla*) (Conservation International 2010). The ecotone between forest and cerrado is also rich in endemic plant species (Fearnside and Ferraz 1995). Unfortunately, this ecosystem has also been widely cleared for soybean expansion as it is the least protected ecosystem in Brazil, with only 1.5% protected within federal reserves (Casson 2003).

15.2.3 Environmental Pollution

Apart from habitat loss, biofuel industries can threaten biodiversity hotspots by causing environmental pollution and degradation through poor farming practices. Inappropriate management practices such as intensive usage of fertilizers and pesticides as well as using fires for land clearing could lead to environmental problems such as soil degradation, and water and air pollution, which in turn could lead to long-term ecological impacts on these biodiversity hotspots. For soybean and sugarcane, which are both annual crops, the ecosystem of the agricultural landscape is disrupted yearly and requires high inputs of fertilizers, pesticides, and weed control to maintain high levels of production (Casson 2003; Martinelli and Filoso 2008). For sugarcane production, bare soils are exposed to intense winds and rains during management practices, which can result in soil erosion rates of up to 30 tons/ha/year (Sparovek and Schnug 2001; Martinelli and Filoso 2008). Soil erosion as a result of soybean cultivation amounts to similar rates of losses between 19 and 30 tons/ha/year depending on soybean management practices, land aspect, and soil type (Tomei and Upham 2009). Mature oil palm plantations in Malaysia have a soil erosion rate of approximately 7.7–14 tons/ha/year (Hartemink 2006). Soil erosion in oil palm plantations can be even more serious in the early years when a complete palm canopy has not yet been established, which is why maintaining a legume crop cover is important to protect against soil erosion (Corley and Tinker 2003).

Surface runoff as a result of soil erosion brings organic matter and agrochemicals into aquatic systems, which can lead to deterioration of aquatic habitats and affect the biodiversity downstream. For example, contaminants such as atrazine, a herbicide used in sugarcane crops, and heavy metals like copper, were found in water samples and stream bed sediments collected from waterways flowing through areas of extensive sugarcane cultivation (Carvalho et al. 1999, Azevedo et al. 2004, Corbi et al. 2006). High levels of nitrogen fertilizer used for sugarcane crops can lead to the excessive accumulation of nitrogen into aquatic systems. Filoso et al. (2003) reported high rates of nitrogen export into rivers draining watersheds such as the Piracicaba and Mogi river basins, which are heavily cultivated with sugarcane. As a legume, soybean cultivation requires little nitrogen inputs but does require agrochemicals to combat diseases, weeds, and pests. The concentration of these agrochemicals in water bodies surrounded by soybean plantations may also accumulate in fish caught for human consumption (Fearnside 2001). Waste products and by-products of the industrial processing of sugarcane and palm oil into ethanol and crude palm oil, respectively, are highly polluting and are a large source of pollution if released into the environment without proper treatment. Palm oil mill effluent and vinasse from sugarcane distillation are rich in organic matter and contribute to eutrophication and depletion of dissolved oxygen levels in aquatic systems if left untreated (Donald 2004; Martinelli and Filoso 2008). Despite the existence of present technologies to treat mill effluents, it is not uncommon for leakages and discharge from small mills to happen, leading to adverse impacts on aquatic ecosystems (Martinelli and Filoso 2008; Sheil et al. 2009).

Burning is a common crop management practice in Brazil for facilitating the harvesting of sugarcane and has been used to clear natural vegetation for oil palm and soybean expansion in Indonesia and Brazil (Casson 2003; Martinelli and Filoso 2008; Sheil et al. 2009). The burning of the straw and leaves of sugarcane greatly facilitates the process of harvesting and drives out snakes, which may pose a danger to the cane cutters (Martinelli and Filoso 2008). However, it also contributes to a higher concentration of suspended aerosols in the atmosphere (Lara et al. 2005) and leads to increases in soil temperature, decreases in soil water content, and soil degradation (Dourdo-Neto et al. 1999; Oliveira et al. 2000; Tominaga et al. 2002).

Oil palm expansion has been partially responsible for the devastating 1997–1998 forest fires in Indonesia, where satellite imagery showed fires were started by oil palm companies to clear land (Dennis et al. 2005). The dry conditions brought about by the El Nino phenomenon exacerbated the fires, which burnt 11.6 million ha of land, more than half of which were montane, lowland, and peat forests (Tacconi 2003). Fires are used to clear forests, because they are a quick and cheap way to clear land (Guyon and Simorangkir 2002) and they lead to forest degradation, which allows oil palm companies to acquire land use permits more easily (Casson 2000). In Brazil, the El Nino effect also led to serious droughts in the North and North-East and fires ignited in the savannah areas for pasture and agricultural crops like soybean blazed out of control, contributing to serious forest fires in the North (Casson 2003).

15.2.4 Interaction with Other Frontier-opening Activities

The development of biofuel plantations is associated with other drivers of habitat loss and degradation such as industrial activities like logging or cattle ranching and the building of infrastructure such as roads and waterways (Fig. 15.1). This increases the accessibility of natural resources for further exploitation and heightens the level of fragmentation and isolation of remnant natural habitats. Oil palm plantations have been associated with logging companies as the profits obtained from the sale of timber can help cover part of the establishment costs of an oil palm plantation (Casson 2000). In cases where companies seek short-term profits or are unwilling to take the risks in developing oil palm industries in infrastructure-poor regions (e.g., Papua and Kalimantan), application for licenses to establish oil palm estates provide a loophole for these companies to clear-cut forests without the use of sustainable management practices for the timber extracted (Casson 2000). This explains why less than 1 million ha out of 5.3 million ha of land allocated to oil palm development have actually been planted with oil palm in

Fig. 15.1 An example of different land uses adjacent to each other – patchwork of legal forest reserves, pasture and soy farms in the Brazilian Amazon (Photo credit: Rhett A. Butler)

Kalimantan (Casson et al. 2007). The expansion of soybean in Brazil has been linked to both charcoal production and cattle ranching (Casson 2003). Soybean expansion provides access to Cerrado trees that are used by the Brazilian steel industry for charcoal production. Profits generated by selling the Cerrado trees to charcoal producers have helped soybean farmers to further soybean expansion. The degradation of gallery forests due to the extraction of such trees has raised concern as these forests provide a corridor that links the Amazon and the coastal forests with the Cerrado and is an important habitat for several endemic fauna (Tengnäs and Nilsson 2003). The advance of large-scale mechanized soybean farms as a result of government policies and soybean technologies pushed small-scale farmers into the Amazonian frontier where agricultural expansion and pasture development took place at the expense of forests (Skole et al. 1994; Schneider et al. 2000). Fearnside (2001) describes how soybean expansion has led to major infrastructure developments in Brazil and highlights the potential for habitat exploitation due to greater accessibility in the region.

In fact, the threats to biodiversity hotspots from biofuel expansion are both direct (habitat replacement and environmental pollution) and indirect (displacement of other activities into natural habitats and increasing accessibility for further exploitation). However, these impacts are not only limited to biofuel production and have surfaced in other agricultural expansion for industry (e.g., rubber, Li et al. 2007; and timber, Fredericksen and Putz 2003) as well as food production (e.g., rice, coffee, cocoa, Donald 2004). The underlying reason for these damaging impacts are poor agricultural practices and policies that focus on the maximization of profits and productivity without taking into consideration the sustainability of the agricultural system and the costs to the environment (IATP 2008). Reducing the biodiversity impacts of biofuel expansion would require a change in production systems and policies and a set of stringent criteria to ensure that biofuels are produced at lower cost to biodiversity and ecological systems. Considering the initial environmental reasons for using biofuels over fossil fuels, it would be a cruel irony if they are to be produced at the expense of biodiverse regions and result in more harm than benefit to the environment.

15.3 How Can We Reconcile Biofuel Expansion with Biodiversity Conservation in These Hotspots?

Reconciling biofuel expansion with biodiversity conservation is not a straightforward process due to the links between the biofuel industry and both the agricultural and energy sector. A careful assessment of land use allocation options and major restructuring of the agricultural management system may be required for biofuel expansion to proceed with little or no environmental costs. Additionally, the development of energy-efficient transportation systems and advancement of second and third generation biofuels will help alleviate demand for conventional biofuel feedstocks. However, these actions will require a considerable amount of time, resources, and long-term commitment from society. From a biodiversity perspective, there is an added urgency to also work on immediate solutions to minimize the loss of threatened biodiversity to biofuel expansion within these hotspots.

15.3.1 Degraded Lands

Clearly, the obvious solution is to avoid planting biofuel feedstocks on native natural habitats (IATP 2008). The replacement of biodiverse habitats with monoculture plantations is without any doubt the greatest threat to biodiversity in these hotspots. Moreover, as many of these hotspots contain high levels of endemic flora and fauna, the loss of these habitats would result in global extinctions of numerous species (Myers et al. 2000). The removal of critical ecosystems for biofuel production negates any benefits accrued from the use of biofuels over fossil fuels (Gibbs et al. 2008). Some researchers have argued for the use of “degraded lands” for biofuel cultivation. However, this proposal is not as straightforward as it seems. Should the definition of “degraded” be stretched to include secondary logged forests, then biodiversity losses will continue; as such, forests still preserve a significant portion of primary forest biodiversity (Dunn 2004; Barlow et al. 2007; Koh and Wilcove 2008). In some cases, degraded lands have been shown to be utilized by high conservation value (HCV) species like the Sumatran tiger and the value of their biodiversity cannot be judged simply based on the vegetation structure and characteristic of the landscape (Maddox et al. 2007). Significant amounts of fertilizers and weed control are also required to convert *alang-alang* grasslands into oil palm plantations (Fairhurst and McLaughlin 2009), and insecure land tenure regarding degraded lands pose big risks to any biofuel feedstock-producing company investing in plantation development (Cotula et al. 2008). Degraded lands can also be open to other land uses such as restoration ecology, cattle ranching, settlements, and urbanization; hence, strategies to expand biofuel production into degraded lands must be approached with caution.

15.3.2 Payment for Ecosystem Services

Apart from their biodiversity values, it is imperative to recognize the ecosystem services natural habitats provide including genetic diversity, carbon sequestration, water cycling and purification, climate regulation, and many other nontimber products that are not found elsewhere (Constanza et al. 1997). The establishment and enforcement of protected areas in biodiversity hotspots remains a top strategic priority for protecting biodiversity, but these legislative tools could be supplemented with innovative schemes, such as Payment for Ecosystem Services (PES) or Reducing Emissions from Deforestation and Degradation (REDD), which create financial incentives to divert agricultural expansion away from forests and onto preexisting croplands or degraded lands. The question that follows then is whether such incentives are sufficient to counter strong market forces that favor natural habitat conversion. Recent REDD scheme partnerships between nongovernmental organizations and private companies (Fischer 2009) are positive steps toward greater collaboration and engagement of various stakeholders toward conserving forests in biodiversity hotspots. However, few studies have compared the feasibility of such schemes against current market prices for biofuel feedstocks. Butler et al. (2009) compared the profitability of converting forests into oil palm plantations against conserving forests for a REDD scheme. Under current voluntary carbon markets, conversion of forest into oil palm plantations (yielding net present values of US$3,835–$9,630 per hectare per year) will be more profitable to landowners than preserving it for carbon credits (US$614–$994). However, should REDD become a legitimate emissions reduction activity under the second commitment period of the Kyoto Protocol (2013–2017), carbon credits traded in Kyoto-compliance markets have a fighting chance to compete with oil palm agriculture or other similarly profitable human activity as an economically attractive land-use option. Similar economic evaluations of comparing the value of nonforest biodiverse habitats like the Cerrado to soybean and sugarcane production in Brazil can also be carried out to determine the competition of various land uses based on monetary values. A recent study conducted by Igari et al. (2009) in the Cerrado region in Sao Paulo State, Brazil demonstrated an annual profitability of US$134/ha/year and US $149/ha/year for sugarcane and soybean crop, respectively. Opportunity costs to set aside the Cerrado for preservation were much higher compared to PES values of US$27 and US$42 per ha paid to landowners in Mexico and Costa Rica, respectively (Munoz-Pina et al. 2008; Barton et al. 2009) and only slightly comparable, US$111 per ha, with the average annual value paid by USDA Conservation Reserve Program in the United States (USDA 2006; Baylis et al. 2008). Considerable amount of research is currently underway to use REDD as a tool against natural habitat conversion by other human land use activities (Mongabay 2010). However, for natural habitats that are already slated for land use conversion, complete avoidance is not a realistic option and strategies to mitigate biodiversity impacts will have to be formulated. There is also the risk that financial lure of REDD might inadvertently cause some landowners to accelerate habitat destruction to raise the deforestation baseline of future REDD projects so that they might reap more monetary benefits (Koh et al. 2009a; Koh 2009). Furthermore, some researchers warn that the indirect and less tangible environmental and socioeconomic implications of PES schemes need to be carefully evaluated (Ghazoul et al. 2010a, b).

15.3.3 Improve Management Practices

To partially reconcile biofuel expansion with biodiversity conservation, a set of compromises regarding biodiversity loss and a great deal of collaboration with biofuel producers will be required. It will be imperative for conservation groups to engage with biofuel producers of various levels – from small farmers to large private companies, to help producers and growers recognize the value and importance of biodiversity in the unique habitats where they grow their biofuel crops. As soybean and sugarcane are annual crops, little can be done to preserve biodiversity within the agricultural landscape when great disturbances to the landscape occur during harvest seasons. Fewer disturbances occur in oil palm plantations, which are perennial crops that last for 25–30 years. In these artificial habitats, Koh (2008a) demonstrated that various local vegetation characteristics such as percentage ground cover of weeds, epiphyte prevalence, and presence of leguminous crops can help enhance native bird and butterfly species richness (Fig. 15.2). On a landscape level, the percentage of natural forest cover was able to explain 1.2–12.9% of variation in butterfly species richness and 0.6–53.3% of variation in bird species richness. Adoption of such measures may make oil palm plantations more hospitable for native biodiversity. Bird-exclusion experiments in oil palm plantations have shown a significant increase in herbivory damage by herbivorous insects, providing an economic justification for conserving remnant natural habitats for this natural pest control service (Koh 2008b). Many oil palm plantations have also included integrated pest management systems that favor the use of nonchemical pest control methods such as the establishment of “beneficial plants” (e.g., *Euphorbia heterophylla*) to attract insect predators and parasitoids of oil palm pests (e.g., the wasp *Dolichogenidea metesae*; Basri et al. 1995; Corley and Tinker 2003). Other means of mitigating the impacts on biodiversity loss within the oil palm plantation landscape include the formation of riparian buffer zones to reduce water pollution, preservation of HCV forests, formation of wildlife buffer zones to “soften” the edge between plantations and natural forests, and the creation of habitat corridors to link remnant forest patches together (Maddox et al. 2007; Fitzherbert et al. 2008). In cases of unavoidable environmental impacts, biodiversity offset schemes could be considered, in which environmental damage to an area could be compensated through the purchase of biodiversity offset credits derived from the conservation of an equitable natural habitat elsewhere (Maddox et al. 2007).

Fig. 15.2 Mature oil palm tree taken from a plantation in Indonesia. The company management followed recommendations of biodiversity friendly practices and left epiphytes to grow around the oil palm stem (Photo credit: Janice S.H. Lee)

15.3.4 Certification Schemes

To ensure that biofuel and biofuel feedstock producers are encouraged to adopt environment-friendly practices, international certification schemes that satisfy a set of social and environmental criteria have been introduced. Creation of multistakeholder organizations such as the Roundtable of Sustainable Biofuels, the Roundtable of Responsible Soy, the Better Sugarcane Initiative, and the Roundtable of Sustainable Palm Oil aim to engage a diverse range of biofuel-sector stakeholders – governments, nongovernmental organizations, producers, consumers, suppliers – to work toward producing biofuel feedstocks using sustainable practices (Laurance et al. 2010). These organizations create, verify, and certify performance standards for sustainable production of biofuel feedstocks and biofuels (UNEP 2009). Within these organizations, conservation groups have a platform to engage and inform producers of suitable new areas for biofuel expansion that will lead to the least ecological damage. Independent Environmental Impact Assessments of future biofuel crop plantings and Life-Cycle Analyses of biofuel products provide greater transparency on the costs of production of biofuels and reassure consumers that biofuels purchased are produced with the best sustainable practices (UNEP 2009). However, critics of biofuel certification schemes argue that market-based product certifications often cover only a fraction of the market size (Sto et al. 2005; Liu et al.

2004; Laurance et al. 2010) and may be misleading as some production appears to be sustainable but in actual fact is not (Doornbosch and Steenblik 2007; Laurance et al. 2010). Most importantly, it has no control over the extent of indirect land-use change resulting from displacement of other land-use activities by biofuel production (Doornbosch and Steenblik 2007).

15.3.5 Designer Landscapes

Addressing the problems arising from indirect land-use changes requires a landscape-level approach where biofuel feedstock production has to be coordinated within the industry and with regional or national land-use plans (Maddox et al. 2007; Koh et al. 2009b). From an ecological perspective, two concepts have been proposed to minimize the adverse impacts of agricultural expansion on biodiversity – land sparing and wildlife-friendly farming. The former seeks to minimize land area required for farming by land intensification through maximizing yields, and the latter tries to enhance biodiversity within an agricultural landscape (Fischer et al. 2008). Koh et al. (2009a, b) proposed a harmonization of both approaches to design landscapes threatened by biofuel expansion based on optimal requirements for sustaining biodiversity, economic, and livelihood needs. Agroforestry (wildlife-friendly farming) zones around HCV areas can be used as corridors to connect surrounding fragments of HCV forests, act as buffer zones to mitigate human encroachment into HCVs, and reduce edge and matrix effects from the intensively cultivated biofuel feedstock landscape (land sparing).

Direct conversion of natural habitats in biodiversity hotspots into agricultural landscapes for biofuel feedstocks is the biggest threat arising from biofuel expansion. There is an urgent need to recognize that all biofuel plantations we reviewed in this chapter are depauperate in biodiversity compared to the natural habitats they replace. Other biofuel feedstocks such as Jatropha and cassava were not explored as there currently exists little research regarding these biofuel crops and their impacts on the environment. Although there are several proposals to reconcile biodiversity conservation with biofuel expansion, these suggestions are still limited in the extent of biodiversity that can be preserved compared to previous natural habitats. Policy makers need to be very aware of how biofuel policies in their countries have the potential to do more harm than good should biofuel production occur at the expense of the world's most biodiverse habitats. Unfortunately, the impact of biofuels is further complicated by the fact that these first generation biofuel feedstocks (soybean, sugarcane, and palm oil) are also important global commodities. Rises in commodity prices as a result of biofuel policies can also trigger expansion on the agricultural front regardless of whether the end use of these commodities is for food, feed, or fuel. Hence, emphasis on multistakeholder collaboration to produce biofuels sustainably and to ensure the protection of remaining natural habitats in biodiversity hotspots is the best immediate remediation to the expansion of biofuels in biodiversity hotspots.

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Chapter 16

Forests of East Australia: The 35th Biodiversity Hotspot

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Abstract The newly identified “Forests of East Australia” Global High Biodiversity Hotspot corresponds with two World Wildlife Fund (WWF) Ecoregions: the Eastern Australian Temperate Forests and Queensland’s Tropical Rain forests. The region contains more than 1,500 endemic vascular plants, meeting the criterion for global biodiversity significance, and more than 70% of natural areas have been cleared or degraded, meeting the criterion for a hotspot. The hotspot, although covering a large latitudinal range (15.5°–35.6° South), has a predominantly summer rainfall pattern with increasing rainfall seasonality northwards into tropical areas of north Queensland. It covers large tracts of elevated tablelands and drier inland slopes, particularly in New South Wales, where it extends inland beyond the New England Tablelands and the Great Dividing Range. Varied soils result in a mosaic pattern of vegetation. Sclerophyllous communities dominated by Australia’s iconic plant, the gum-tree (*Eucalyptus* species), are the most prevalent vegetation type. Significant areas of rain forest exist throughout the region, much of which has persisted continuously since Gondwanan times, providing a rich living record of evolution over more than 100 million years. The human population of the hotspot as of 2006 was over nine million, with a population density of 36 people per square kilometer, mainly concentrated along the coast. About 18% of the land area is under some form of formal protection for its natural values. Gaps in the protected area network include some centers of plant endemism and some areas of critical habitat for threatened species. Whole of landscape conservation initiatives are enhancing connectivity throughout the Great Dividing Range through voluntary protection and restoration programs.

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Vital Signs

Hotspot Original Extent (sq. km.)	253,200
Hotspot Primary Vegetation Remaining (sq. km.)	58,900
Plant Species	>8,257
Endemic Plant Species	>2,144
Vertebrate Species	>1,141
Endemic Vertebrate Species	>152
Area Protected (km^2)	46,600
Area Protected within IUCN categories I–IV (km^2)	41,300

16.1 Overview

When the hotspots concept was first developed by Myers (1988), he included the Queensland Wet Tropics as one of his ten original hotspots, in large part because of its high plant endemism. Later, in the second major revision of the hotspots concept (Mittermeier et al. 2004), the Queensland Wet Tropics was given an "honorable mention" chapter (Stanton et al. 2004), even though it fell short of meeting the cutoff criteria for full hotspots status. Subsequently, on comparing the size of the Queensland Wet Tropics to other hotspots, and recognizing that it represented only a small portion of a much larger forested area in eastern Australia, the authors decided that further analysis was necessary to see if this larger Australian forest complex merited inclusion on the hotspots list. This analysis, led by the Australian co-authors of this chapter, determined without a doubt that the Forests of East Australia should be added to the list as the 35th hotspot. The results of this analysis are presented here.

The newly identified Forests of East Australia Hotspot consists of a discontinuous coastal stretch along the Australian states of Queensland and New South Wales, extending inland and further west, although it does include the New England Tablelands and the Great Dividing Range. Its boundaries correspond to a combination of two World Wildlife Fund (WWF) Ecoregions: the Eastern Australian Temperate Forests and Queensland's Tropical Rain Forests (Fig. 16.1).

The hotspot, although covering a large latitudinal range (15.5°–35.6° South), has a predominantly summer rainfall pattern with increasing rainfall seasonality northwards into the tropical areas of north Queensland. Annual rainfall is unpredictable from year to year varying on average between 550 mm in the more arid savanna regions to 4,500 mm near the tropical coast. Mountain tops in the northern "Wet Tropics" region have recorded annual rainfall events in excess of 12,000 mm. Temperatures are also variable, with annual winter snowfalls at high elevations in the south and a tropical climate in the far north. Altitudinal variation is from sea level to about 1,600 m. The hotspot covers a broad range of environments including flat to rolling and undulating coastal plains; riverine and estuarine systems with accompanying deltas or floodplains; foothills of adjacent coastal ranges; coastal and mountain range escarpments, some with exposed summits and peaks; elevated

Fig. 16.1 Forests of East Australia Hotspot. Follows the boundaries of two WWF Ecoregions: the Queensland Tropical Rain forests in the north and the Eastern Australian Temperate Forests in the south

tablelands; undulating drier inland slopes and plains, particularly in north-west New South Wales; and naturally occurring freshwater lagoons and lakes.

The dominant rock types include Mesozoic sandstones and acid igneous rocks, with relatively recent basalts in the north. Varied soils result in a mosaic pattern of vegetation, with infertile soils throughout much of the hotspot, except for localized basalt-derived soils which are thinly spread throughout the latitudinal range of the hotspot. Sclerophyllous communities dominated by Australia's iconic plant, the gum-tree (*Eucalyptus* species), are the most prevalent vegetation type. Significant areas of rain forest exist throughout the region, much of which has existed continuously since Gondwanan times, providing a rich living record of evolution during well over 100 million years. In higher rainfall area on more fertile soils, forest trees can reach 70 m high. In both lower rainfall and subalpine areas, grasses and herbs become more dominant within grassy woodlands with eucalypts only 8–15 m high.

16.2 Methods

16.2.1 Plant Diversity and Endemism

Vascular plant records were compiled from the Australian National Herbarium (2005) and Queensland Herbarium (2003). Nomenclature follows Henderson (Henderson 2002) where applicable, or otherwise Stevens (2001 onward). A taxon was determined to be endemic to the hotspot if it was known from more than ten records and completely within the region of interest, or >50 records and

95% within the region. Taxa were defined as probably endemic if known from < 10 records, completely within the region of interest or <50 records and 88% within the region. Some taxa were defined as requiring further assessment where there were less than five records with >70% occurring within the region. Formal and popular literature were used to validate the status of some species, including The Flora of New South Wales (Harden 1990–1993), the Queensland Census (Henderson 2002), Fairley and Moore (1989) from the Sydney Region, The Native Vegetation of New South Wales (Keith 2004), Fruits of the Rainforest (Cooper 2004), Rainforest Trees of Southeast Australia (Floyd 1989), Flora of Australia (Pteridophytes) (ABRS/CSIRO Australia 1998), and Eucalypts (Brooker and Kleinig 1994). Taxa with manuscript names were not considered. Taxa that satisfied the above criteria were then further scrutinized with the use of the above-mentioned literature. Such an approach reduced the effect of inaccurate locality information and geocodes.

16.2.2 Vertebrate Diversity and Endemism

For birds and reptiles, we used data compiled in the Australian Natural Heritage Assessment Tool (ANHAT) current to August 2006 (Department of Environment and Heritage 2006). Vertebrate taxonomy was based on the Australian Faunal Directory (ABRS 2006). To allow for varying levels of spatial precision, distribution records were summarized to a grid of 10 × 10 km cells covering the hotspot. Records collected before 1950 or with a potential spatial error >20 km were excluded from the analysis (see Slatyer et al. 2007) for more details on data preparation for an Australia-wide endemism analysis). Species with <3 records within the hotspot were assumed to be erroneous or vagrant and excluded from the hotspot species list, unless these records were the only ones for the species. In the latter case, further checks were performed to confirm the species endemism within the region. Allowing for a small percentage of erroneous records, species were found to be endemic to the hotspot if known from ≥50 records with ≥95% of these records occurring within the hotspot or if known from 10–50 records with 100% of these within the hotspot. Species with <10 records or that just missed inclusion based on the above thresholds were subject to manual checking. Species found to be endemic were verified using published distribution information.

For consistency with other regions, the numbers for mammals and amphibians presented here are from a larger reanalysis for all hotspots based on the most recent IUCN Global Mammal Assessment and Global Amphibian Assessment (see chapter 1, Mittermeier et al., 2011). However, we also obtained results for mammals and amphibians using the methods described above for birds and reptiles. This more precise analysis yielded similar results to the IUCN Red List analysis. Both analyses yielded much higher estimates of total numbers of species and percent endemism than data obtained through WWF WildFinder (WWF 2006).

16.2.3 Primary Vegetation Extent

The extent of primary vegetation is a criterion, along with the number of endemic vascular plants, in classifying a region as a global high biodiversity hotspot (Myers et al. 2000). We consider primary vegetation to be relatively pristine natural areas in which the majority of species and ecological processes are intact. Spatial analysis of amount and percent of primary vegetation remaining in the hotspot was based on data classified as “residual” by the Vegetation Assets, States and Transitions (VAST) framework (Fig. 16.2, Table 16.1). The VAST framework orders vegetation by degree of anthropogenic modification as a series of condition states, from a residual or baseline condition through to total removal (Thackway and Lesslie 2006; Thackway and Lesslie 2008). The residual classification corresponds well with the definition of primary vegetation.

16.2.4 Land Use

Spatial analysis of amount and percent of land use classes in the hotspot (Table 16.3) was based on the catchment-scale land use mapping for Australia (Bureau of Rural Sciences 2009) which applies the Australian Land Use and Management Classification (ACLUMP 2006).

16.2.5 Area Protected

Spatial analysis of amount and percent of hotspot area under formal protection (Table 16.4) was based on the Collaborative Australian Protected Areas Database current to 2006 (Department of the Environment Water Heritage and the Arts 2009).

16.3 Unique Biodiversity

A number of prehistoric events were responsible for the high levels of diversity and endemism found in the Forests of East Australia Hotspot. Geographic isolation of this region over millions of years resulted in sclerophyllous flora evolving from ancestral rain forest stock on nutrient-depleted soils, and desertification of central Australia promoted further speciation. Speciation within rain forest flora occurred in Gondwanan elements, gymnosperms, and basal lineage angiosperms. Subsequently, floral and vertebrate migrations occurred from the Indonesian plate, increasing with lowered sea level during periods of glaciation. Although many higher order taxa from the region have been catalogued, much of the biodiversity of the hotpot, as for the rest of Australia, remains unknown to science.

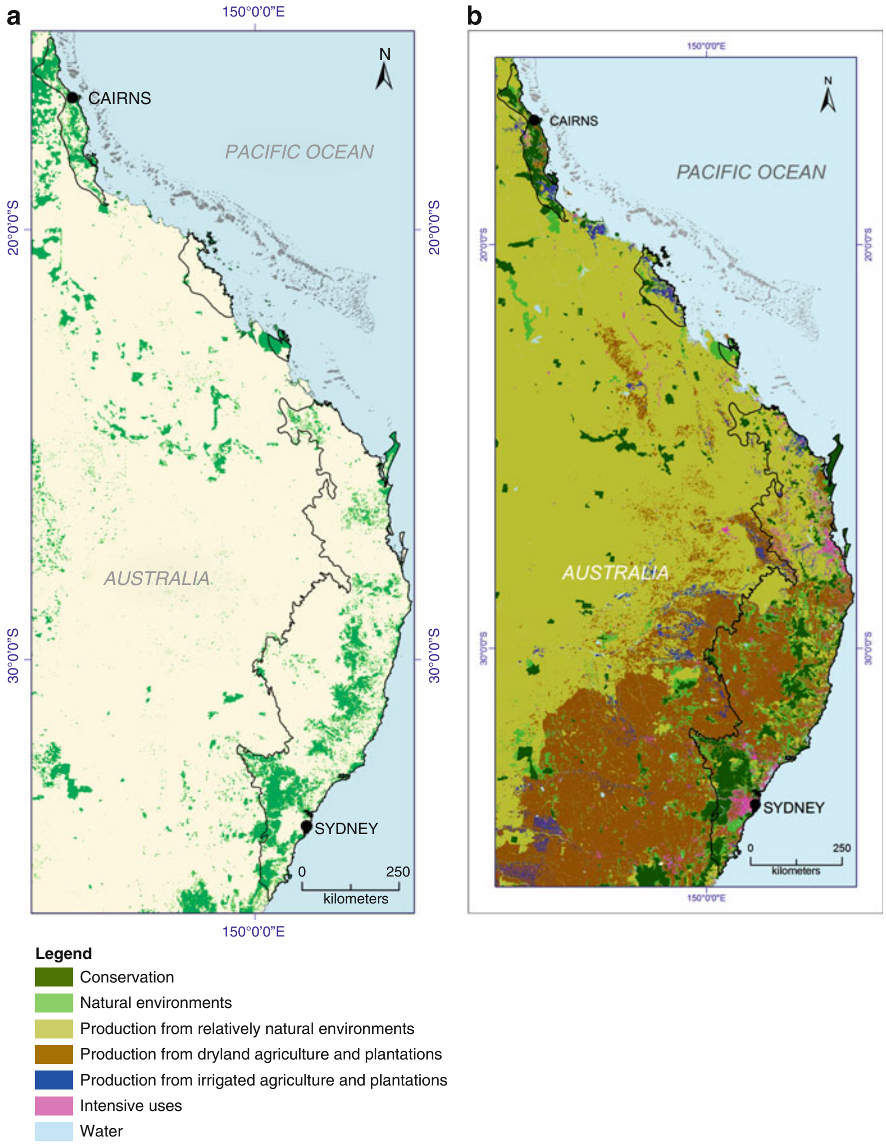


Fig. 16.2 (**a**) Extent of primary vegetation in the Forests of East Australia Hotspot (*source*: Thackway and Lesslie 2008). (**b**) Landuse in the Forests of East Australia Hotspot (*source*: Bureau of Rural Sciences 2009)

16.3.1 Plants

The hotspot consists of both rain forest and sclerophyllous communities with the sclerophyllous vegetation being dominant. Of 8,257 species of vascular plants, at

Table 16.1 State of native vegetation in the Forests of East Australia Hotspot (after Lesslie et al. 2008; Thackway and Lesslie 2006; Thackway and Lesslie 2008). Primary forest remaining in the hotspot is defined as the residual and naturally bare class

Category	Vegetation State	Area (km^2)	Percent of total
Residual and naturally bare	Native vegetation structure, composition, and regenerative capacity intact, including areas that are naturally bare or naturally disturbed; not significantly perturbed by land use / land management practice	58,900	23.3
Modified	Native vegetation community structure, composition, and regenerative capacity intact, but perturbed by land use/ and management practice	65,300	25.8
Transformed	Native vegetation community structure, composition, and regenerative capacity significantly altered by land use/land management practice	6000	2.4
Replaced-Managed	Native vegetation replaced with cultivated vegetation	120,300	47.5
Removed	Vegetation removed – alienation to nonvegetated land cover	2,600	1.1
Total		253,200	100

Table 16.2 Species diversity and endemism recorded for the Forests of East Australia Hotspot

Taxonomic Group	Species	Endemic species	Percent endemism	Endemic genera[c]	Endemic families
Plants – Flowering (dicots)	5,884	1,731	29.4	73	1
Plants – Flowering (monocots)	1,917	294	15.3	22	2
Plants – Gymnosperms	71	35	49.3	2	0
Plants – Ferns and allies	385	84	21.8	2	0
Vascular Plants – total	>8,257	>2,144	25.9	99	3
Birds	549	28	5.1	3	0
Mammals	133	6[a]	4.5	0	0
Amphibians	120	38[a]	31.7	4[b]	0
Reptiles	259	70	27.0	14	0
Freshwater Fish	>80	>10	12.5	>?	>?
Vertebrates – total	>1,141	>152	13.3	>21	>?

[a] The analysis described in Sect. 16.2.2 yielded higher total numbers of endemic species for mammals (12) and amphibians (43) than shown. While these higher numbers are likely more accurate, we used the IUCN analysis here for consistency with other regions

[b] One amphibian genus included in this count, *Rheobatrachus*, is probably extinct, giving 3 extant amphibian genera

[c] Endemic genera listed in Appendix 1 by family

least 2,144 are endemic (26%); exceeding the 1,500 endemic species required for a biodiversity hotspot (Table 16.2). Surprisingly, only 99 of 2,031 genera (5%) are endemic, but a further 26 genera may include some endemics following further review of their status. Of particular note is the fact that three families occur nowhere else in the world (Doryanthaceae and the monotypic Austrobaileyaceae and Petermanniaceae). This is a very high level of plant endemism at the family level, and places this hotspot second or third among all hotspots in this category. One member of the Doryanthaceae family, the Giant or Gymea Lily (*Doryanthes excelsa*), has edible roots and flower spikes, traditionally eaten roasted by Aboriginal people (see Fig. 16.3). Basal angiosperms are a conspicuous component of the rain forest flora, with both *Austrobaileya* (see Fig. 16.3) and *Trimenia* (Trimeniaceae) being members of the ANITA grade of magnoliids.

The hotspot is also home to the recently discovered and Critically Endangered Wollemi Pine (*Wollemia nobilis*), which has fewer than 50 mature individuals. It is considered a living fossil, with all other members of its genus extinct for over 2 million years. This species is restricted to the Wollemi National Park, within the Blue Mountains World Heritage Area (Fig. 16.3).

The hotspot harbors 32 globally threatened plant species according to the 2009 IUCN Red List (IUCN 2009): one Critically Endangered, 12 Endangered, and 19 Vulnerable. It also contains 27% of the 1,296 plant species considered rare or threatened in Australia by the *Environmental Protection and Biodiversity Conservation Act 1999* (the EPBC Act).

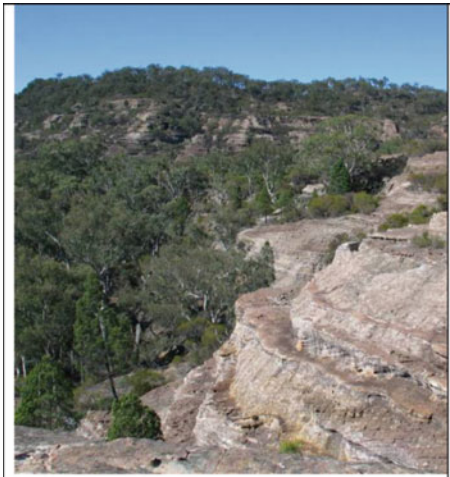
16.3.2 Vertebrates

Overall vertebrate endemism is about 13%, including information for amphibians, reptiles, birds, mammals, and freshwater fish. Of vertebrate species in the hotspot, amphibian species endemism is the highest (32%; Table 16.2). However, there have been several amphibian extinctions in the recent past, with the extinction of the two remarkable species of gastric-brooding frog being the most noteworthy. More hopeful is the story of the Yellow-Spotted Bellfrog (*Litoria castanea, CR*). The species had not been sighted since 1980, and was thought to have declined mainly due to chytridiomycosis. Widely thought to be extinct, the species was recorded in 2008 and a population of about 100 was confirmed in 2009. Possible resistance to chytridiomycosis of remaining individuals is being studied.

Reptile endemism is also high (27%; Table 16.2). One endemic reptile, the rain forest-dwelling Boyd's Forest Dragon (*Hypsilurus boydii*), is unusual in that its body temperature is generally within one degree of air temperature (see Fig. 16.3).

A total of 28 out of 549 birds (5%) are considered endemic (Table 16.2). The extraordinary colorful Paradise Parrot (*Psephotus pulcherrimus*) was likely endemic to the hotspot, but is considered extinct, with the last sighting in 1927. The species fed mainly on grass seeds and nested in hollowed termite mounds. The cause of extinction is unknown, but contributing factors may have included trapping and egg collection, disease, predation by introduced mammals, changes to the fire regime, and reduction of food supply due to overgrazing and land clearing.

We estimate that well over 80 freshwater fish species are present in the hotspot, of which over 10 (or approximately 13%) are endemic (Unmack 2001; Wet Tropics Management Authority 2010; Table 16.2). These numbers are almost certainly underestimates, and further analysis of freshwater fish data using finer-scale basin



The Wollemi National Park is the only place where the Wollemi Pine (*Wollemia nobilis*, CR) is known to occur.

D oryanthes excelsa, a member of the endemic Doryanthaceae family, has a number of traditional uses.

Hinchinbrook Island, in the Wet Tropics of Queensland.

Austrobaileya scandens is a member of a family endemic to the Forests of East Australia Hotspot.

Wet sclerophyll forest occurs in the higher rainfall areas of the hotspot. At Crediton, west of Mackay, the dominant tree species is *Eucalyptus grandis* (Flooded Gum), which achieves heights of 80m.

Boyd's Forest Dragon (*Hypsilurus boydii*) is found only in the wet tropics of Queensland.

Fig. 16.3 Example landscapes, flora and fauna in the Forests of East Australia Hotspot

Table 16.3 Primary land use types in the Forests of East Australia Hotspot (ACLUMP 2006, Bureau of Rural Sciences 2009)

Land uses	Area (km$^{2)}$	Percent of total
Conservation and natural environments	82,200	32.5
Intensive land use (urban and agricultural)	13,700	5.4
Production from dryland agriculture and plantations	70,400	27.8
Production from irrigated agriculture and plantations	5,700	2.3
Production from relatively natural environments	75,600	29.9
Water	5,600	2.2
Total	253,200	100

Table 16.4 IUCN categories of protection in the Forests of East Australia Hotspot (Department of the Environment Water Heritage and the Arts 2009)

IUCN category	Area (km^2)	Percent of total
I: Strict Nature Reserve	15,800	6.24
II: National Parks	25,200	9.96
III: Natural Monument	200	0.09
IV: Habitat/species Management Area	100	0.04
V: Protected Landscape	100	0.04
VI: Managed Resource Protected Area	5,200	2.04
Total	46,600	18.40

data is needed to generate a more accurate estimate of diversity and endemism within the hotspot boundaries.

16.4 Human Impact

The human population of the hotspot as of 2006 was 9,147,190, with a population density of 36 people per square kilometer (see Mittermeier et al. 2011) for details on this analysis, which utilized LandScan™ GP2007 data (ORNL 2007). Much of the population is concentrated along the coast.

Approximately 58,900 km^2 (23%) of the hotspot comprises primary vegetation (Table 16.1). This analysis used data compiled between 1995 and 2003 (Thackway and Lesslie 2008) to determine that more than 70% of the total land area of the hotspot has lost its primary vegetation. More than 65% of the hotspot is under some form of production land use (Fig. 16.3, Table 16.3).

In the north of the hotspot, within the Queensland Tropical Rain Forests Ecoregion, major threats include invasive pest species and habitat fragmentation, although substantial areas are now protected in the Wet Tropics World Heritage Area. Fragmentation within forest patches through road and powerline construction also increases the spread of invasive species and facilitates the entry of fire. *Phytophthora cinnamomi*, a highly invasive, soil-borne water mold, has resulted in significant rain forest dieback at some sites. Pollution from agricultural runoff is an additional threat. The Ecoregion itself is listed by WWF as "Vulnerable" (Olson and Dinerstein 2002).

Human impact is even higher further south, within the Eastern Australian Temperate Forests Ecoregion, listed by WWF as "Critical/Endangered" (Olson and Dinerstein 2002). Population density is higher in this part of the hotspot, and major threats are related to ongoing clearing of native vegetation for urban development, introduced species, altered fire regimes, water pollution, and schemes for water use.

Threats within protected areas throughout the hotspot include tourism, altered fire regimes, sewage disposal, and invasive plants and animals. Specific threats to amphibians include chytridiomycosis, which is suggested as a cause for a number of recent species extinctions and was first detected as a major threat to amphibian species in Queensland in the 1990s.

16.5 Conservation Actions

A combined total of about 46,600 km^2 (18%) of the land area in the Forests of East Australia Hotspot is under some form of formal protection, with a total of 41,300 km^2 (16%) falling within IUCN protected area categories I–IV (Table 16.4). The Royal National Park, south of Sydney, was the second proclaimed National Park in the world. Fraser Island, the Blue Mountains, the Gondwana Rain Forests, and the Wet Tropics of Queensland are all UNESCO World Heritage Areas (e.g., Hinchinbrook Island, see Fig. 16.3) and the Noosa region is a UNESCO Biosphere Reserve. Gaps in the protected area network include some centers of plant endemism and some areas of critical habitat for threatened species.

Recent reductions in rabbit populations in the tablelands of New South Wales and other areas and the introduction of voluntary habitat protection schemes on farms have led to the recovery of some native vegetation. The cessation of broadscale clearing in Queensland at the end of 2006 will lead to a further reduction in the rate of loss of native vegetation, though the condition of remnants in production landscapes has continued to decline (Wilson et al. 2008). Biodiversity has become increasingly vulnerable because of loss of habitat extent and reduced ecosystem resilience, possibly aggravated by enhanced climatic variability (Beeton et al. 2006). Community-based landscape restoration programs, such as the Great Eastern Ranges initiative (NSW Australian 2010) and environmental stewardships (Government 2010; Wilson et al. 2008) are increasingly important mechanisms, assisting land managers to protect the natural environment.

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Appendix 1: List of Genus-level Endemic Vertebrate Animals (Excluding Freshwater Fish) and Vascular Plants Known from the Forests of East Australia Hotspot

Vertebrate group	Family	Genus
Birds	Acanthizidae	Oreoscopus
Birds	Acanthizidae	Origma
Birds	Ptilonorhynchidae	Scenopoeetes
Amphibians	Myobatrachidae	Taudactylus
Amphibians	Myobatrachidae	Rheobatrachus*
Amphibians	Myobatrachidae	Assa
Amphibians	Myobatrachidae	Adelotus
Reptiles	Elapidae	Tropidechis
Reptiles	Elapidae	Cacophis
Reptiles	Gekkonidae	Phyllurus
Reptiles	Gekkonidae	Carphodactylus
Reptiles	Scincidae	Calyptotis
Reptiles	Scincidae	Gnypetoscincus
Reptiles	Scincidae	Ophioscincus
Reptiles	Scincidae	Harrisoniascincus
Reptiles	Scincidae	Coeranoscincus
Reptiles	Scincidae	Eroticoscincus
Reptiles	Scincidae	Saiphos
Reptiles	Scincidae	Coggeria
Reptiles	Scincidae	Nangura
Reptiles	Chelidae	Elusor

Vascular plant group	Family	Genus
Flowering (dicots)	Akaniaceae	Akania
Flowering (dicots)	Alseuosmiaceae	Crispiloba
Flowering (dicots)	Anacardiaceae	Rhodosphaera
Flowering (dicots)	Araliaceae	Cephalaralia
Flowering (dicots)	Araliaceae	Motherwellia
Flowering (dicots)	Austrobaileyaceae	Austrobaileya
Flowering (dicots)	Celastraceae	Hedraianthera
Flowering (dicots)	Celastraceae	Hexaspora
Flowering (dicots)	Celastraceae	Hypsophila
Flowering (dicots)	Cunoniaceae	Acrophyllum
Flowering (dicots)	Cunoniaceae	Davidsonia
Flowering (dicots)	Cunoniaceae	Pseudoweinmannia
Flowering (dicots)	Cunoniaceae	Vesselowskya
Flowering (dicots)	Elaeocarpaceae	Peripentadenia
Flowering (dicots)	Ericaceae	Rupicola
Flowering (dicots)	Euphorbiaceae	Hylandia
Flowering (dicots)	Euphorbiaceae	Rockinghamia
Flowering (dicots)	Fabaceae	Almaleea
Flowering (dicots)	Flacourtiaceae	Baileyoxylon
Flowering (dicots)	Flacourtiaceae	Streptothamnus
Flowering (dicots)	Gesneriaceae	Lenbrassia
Flowering (dicots)	Grossulariaceae	Cuttsia
Flowering (dicots)	Hamamelidaceae	Neostrearia
Flowering (dicots)	Hamamelidaceae	Noahdendron
Flowering (dicots)	Hamamelidaceae	Ostrearia
Flowering (dicots)	Icacinaceae	Irvingbaileya
Flowering (dicots)	Loranthaceae	Atkinsonia
Flowering (dicots)	Loranthaceae	Benthamina
Flowering (dicots)	Meliaceae	Synoum
Flowering (dicots)	Menispermaceae	Echinostephia
Flowering (dicots)	Monimiaceae	Austromatthaea
Flowering (dicots)	Monimiaceae	Endressia
Flowering (dicots)	Monimiaceae	Hemmantia
Flowering (dicots)	Myrtaceae	Anetholea
Flowering (dicots)	Myrtaceae	Austromyrtus
Flowering (dicots)	Myrtaceae	Barongia
Flowering (dicots)	Myrtaceae	Choricarpia
Flowering (dicots)	Myrtaceae	Lenwebbia
Flowering (dicots)	Myrtaceae	Mitrantia
Flowering (dicots)	Myrtaceae	Ristantia
Flowering (dicots)	Myrtaceae	Sphaerantia
Flowering (dicots)	Myrtaceae	Stockwellia
Flowering (dicots)	Myrtaceae	Tristania
Flowering (dicots)	Myrtaceae	Waterhousea
Flowering (dicots)	Proteaceae	Athertonia
Flowering (dicots)	Proteaceae	Austromuellera
Flowering (dicots)	Proteaceae	Buckinghamia
Flowering (dicots)	Proteaceae	Cardwellia

(continued)

Vascular plant group	Family	Genus
Flowering (dicots)	Proteaceae	Carnarvonia
Flowering (dicots)	Proteaceae	Catalepidia
Flowering (dicots)	Proteaceae	Darlingia
Flowering (dicots)	Proteaceae	Eidothea
Flowering (dicots)	Proteaceae	Floydia
Flowering (dicots)	Proteaceae	Hicksbeachia
Flowering (dicots)	Proteaceae	Hollandaea
Flowering (dicots)	Proteaceae	Megahertzia
Flowering (dicots)	Proteaceae	Musgravea
Flowering (dicots)	Proteaceae	Neorites
Flowering (dicots)	Proteaceae	Opisthiolepis
Flowering (dicots)	Proteaceae	Placospermum
Flowering (dicots)	Proteaceae	Sphalmium
Flowering (dicots)	Proteaceae	Triunia
Flowering (dicots)	Rhamnaceae	Schistocarpaea
Flowering (dicots)	Rubiaceae	Durringtonia
Flowering (dicots)	Rutaceae	Brombya
Flowering (dicots)	Rutaceae	Pentaceras
Flowering (dicots)	Sapindaceae	Castanospora
Flowering (dicots)	Sapindaceae	Sarcotoechia
Flowering (dicots)	Sterculiaceae	Franciscodendron
Flowering (dicots)	Surianaceae	Guilfoylia
Flowering (monocots)	Anthericaceae	Alania
Flowering (monocots)	Arecaceae	Laccospadix
Flowering (monocots)	Arecaceae	Normanbya
Flowering (monocots)	Arecaceae	Oraniopsis
Flowering (monocots)	Asteliaceae	Neoastelia
Flowering (monocots)	Convallariaceae	Kuntheria
Flowering (monocots)	Convallariaceae	Tripladenia
Flowering (monocots)	Cyperaceae	Ptilothrix
Flowering (monocots)	Doryanthaceae	Doryanthes
Flowering (monocots)	Juncaginaceae	Maundia
Flowering (monocots)	Orchidaceae	Cooktownia
Flowering (monocots)	Orchidaceae	Corunastylis
Flowering (monocots)	Orchidaceae	Corymborkis
Flowering (monocots)	Orchidaceae	Papillilabium
Flowering (monocots)	Orchidaceae	Peristeranthus
Flowering (monocots)	Orchidaceae	Rimacola
Flowering (monocots)	Orchidaceae	Schistotylus
Flowering (monocots)	Petermanniaceae	Petermannia
Flowering (monocots)	Poaceae	Alexfloydia
Flowering (monocots)	Poaceae	Notochloe
Flowering (monocots)	Poaceae	Potamophila
Flowering (monocots)	Restionaceae	Coleocarya
Gymnosperms	Araucariaceae	Wollemia
Gymnosperms	Zamiaceae	Lepidozamia
Ferns and allies	Blechnaceae	Pteridoblechnum
Ferns and allies	Dryopteridaceae	Revwattsia

*Probably extinct

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Chapter 17
Status and Threats in the Dynamic Landscapes of Northern Australia's Tropical Rainforest Biodiversity Hotspot: The Wet Tropics

Nigel E. Stork, Steve Goosem, and Stephen M. Turton

Abstract Tropical rainforests throughout the world are highly contested landscapes as governments and the commercial sector seek to increase economic benefits from them. Major threats include logging, both legal and illegal, fire and general encroachment through increased access. Australia's rainforests comprise a miniscule proportion of this total but are vitally important for their unique biodiversity. The largest fragment of tropical rainforest in Australia occurs as a narrow strip along the east coast from 15°30′S to almost 19°25′S and covers approximately two million hectares. Such is the biological significance of the largest section of rainforest, the so called Wet Tropics, that it was inscribed as the Wet Tropics of Queensland World Heritage Area in 1988. This area forms a small part of the recently recognised Forests of East Australia biodiversity hotspot. European settlement has brought about radical change to the Wet Tropics, displacing traditional management by Indigenous Australians. In the last 50 years, our understanding of the region and the threats to it has increased enormously. Logging has ceased, yet threats from invasive species, internal fragmentation and linear infrastructure are still apparent. Climate change looms as a source of a range of threats that the Wet Tropics is ill prepared to face.

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17.1 Introduction

Australia is recognised by the World Conservation Monitoring Centre as one of the world's 17 mega-diverse countries, which collectively harbour 75% of the earth's total biological diversity (Australia State of the Environment Report 2001). It is also home to two of the world's recognised 35 terrestrial biodiversity hotspots (Mittermeier et al. 2011; Williams et al. 2011). Where it differs from the other mega-diverse countries is that its population density is so remarkably low. With such a low density, should the threats to Australia's biodiversity and the challenges of managing this biodiversity be minimal? Here, by focusing on the tropical rainforests in the north-east of this continent, we show that this is not the case and that there are some important lessons to be learnt from the Australian experience. We also look at the importance of Australia's rainforests to both global and regional biodiversity. Although they comprise less than 1% of the total area of the continent of Australia, they are seen as vitally important for their unique biodiversity, for the unique ecosystem they represent in what is a very dry continent, and because they are the last vestiges of what was an ancient and extensive ecosystem, covering perhaps as much as a third of Australia in the geological past. The range of climates in which they have survived is exceptionally wide and the number of plants and animals that are endemic to them and are still identifiable as being of very primitive stocks is scientifically exciting. In this chapter, we focus on the Wet Tropics rainforests which cover about 5% of the Forests of East Australia biodiversity hotspot (Williams et al. 2011) – we do so because much of the endemic biodiversity of this global biodiversity hotspot is located in the Wet Tropics and because of its biological, social and cultural significance as recognised by its world heritage status. This area of rainforest has been the subject of much scientific scrutiny and debate as summarised extensively elsewhere (Stork and Turton 2008).

Moist tropical rainforests cover approximately 6–7% of the land surface of the globe and occur in a band about 15–20° either side of the equator. Typically, they receive more than 2,000 mm precipitation a year and may frequently experience a dry season, although this is often punctuated by periods of heavy rainfall. These forests are typified by their evergreen nature although some species of trees can be deciduous or semi-evergreen. Longer dry seasons inevitably produce tropical dry forests with most tree species being deciduous or semi-evergreen. It is often said that tropical rainforests house more than half of the world's biodiversity; notably at least 44% of the world's vascular plants and 35% of the world's vertebrates (Sechrest et al. 2002) are endemic to 25 "global biodiversity hotspots" (Myers et al. 2000), more than half of which are rainforest sites.

17.2 Australian Forests

Australia is an exceptionally dry continent in a global context. However, northern regions of Australia receive monsoonal rains and support patches of rainforest (Fig. 17.1) (Bowman 2000; McKenzie et al. 1991). In some parts of Australia's east coast where the mountainous Great Dividing Range meets the coast, rainfall can average ≥3,000 mm/year. This is the area mostly covered by the Forests of East Australia biodiversity hotspot (Williams et al. 2011), but also includes some rainforests in Victoria and Tasmania (see Table 17.1). Although much of the eastern Australia coastline is or was forested, rainforest occurs only where there is high annual rainfall and also where there is sufficient rain to maintain soil moisture during the dry season (more than 50 mm in any month). As a result, rainforests are scattered throughout tropical, subtropical, warm temperate and cool temperate areas of Queensland, New South Wales, Victoria and Tasmania, with small patches also found in north coastal Northern Territory and Western Australia. Rainforests occur from sea level to high altitudes, usually within 100 km of the coast in areas receiving more than 1,200 mm of annual rainfall that are climatic and fire proof refuges. Figure 17.1 (after Bowman 2000) shows just how fragmented the distribution of rainforests in Australia is today. Not surprisingly, these forests have been the focus of much research on forest fragmentation (Laurance and Bierregaard 1997;

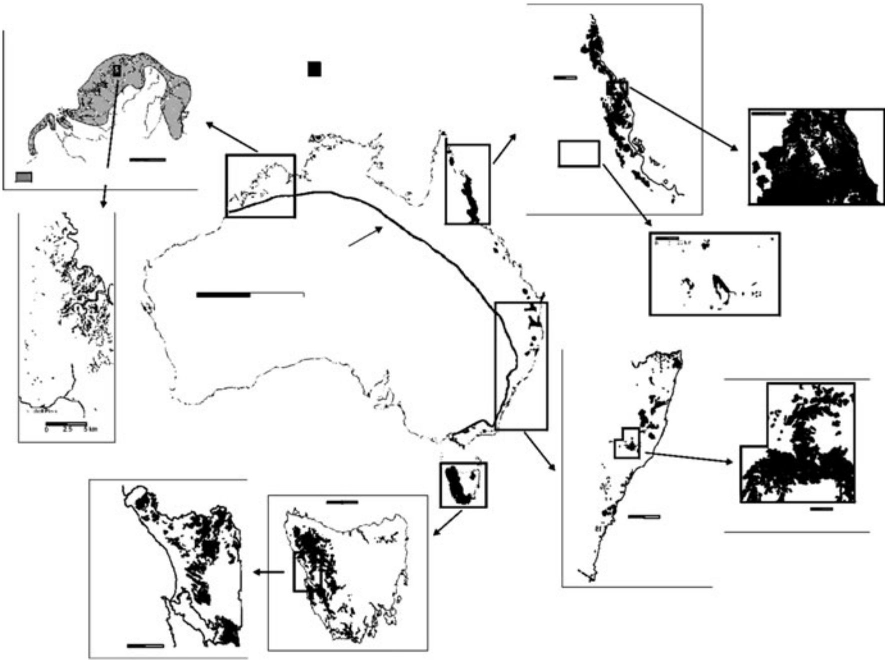

Fig. 17.1 Map of extent of rainforests in Australia (after Bowman 2000)

Table 17.1 Area of pre-European and present day rainforest in Australia (km^2) and % contribution of the different States to the present extent of rainforest

	State						Continent	Region
	VIC	WA	NSW	NT	TAS	QLD	Australia	Wet Tropics
Present area	407	16	2,218	977	7,055	19,558	30,231	8,340
Pre-European estimate	445	18	4,836	978	7,161	30,055	43,493	10,974
Percent remaining	91.5	88.9	45.9	99.9	98.5	65.1	69.5	76
Contribution of states to present extent of rainforest (%)	13	0.1	7.3	3.2	23.3	64.7	100	22.1

Source: National Land and Water Resources Audit (2001), WTMA (2002) and Stork et al. (2008)

Laurance and Goosem 2008). Only about 19% or 147 million hectares of Australia has a native forest cover (BRS 2003), of which just over three million hectares is rainforest. The largest area of remaining rainforest in Australia is located in the north-east in the so called Wet Tropics region (27.6%).

An estimated 30% (~13,000 km^2) of the pre-European extent of Australian rainforests has been cleared (National Land and Water Resources Audit 2001), but certain rainforest systems have been more adversely affected than others. Most accessible lowland and upland rainforests have been cleared and/or have become highly fragmented, while most remaining larger blocks of rainforest are now confined to steep or rugged terrains. Historically, rainforests were among the earliest Australian native vegetation communities to be exploited for timber and agriculture. Examples of extensive past rainforest clearing include the decimation of the “Big Scrub” sub-tropical rainforests in northern New South Wales (Frith 1977), the warm temperate Illawarra rainforests (Strom 1977), the hoop pine scrubs of south-east Queensland (Young and McDonald 1987), the rainforests of the Atherton and Eungella Tablelands, the coastal floodplain rainforests of the Daintree, Barron, Johnstone, Tully-Murray, Herbert, Proserpine and Pioneer rivers in north-east Queensland and extensive areas of Brigalow Belt vine thickets in Queensland and New South Wales (Sattler and Williams 1999). In recent years, there has been strong opposition to such clearing from the conservation sector and this has lead to “Regional Forest Agreements” with governments and industry in key locations in eastern and southern Australia penetrating large areas of rainforest as well as other forest types.

The broad range of ecological community types classified under the umbrella term “rainforest” masks the level of regional depletion of some rainforest and vine thicket types. In the Wet Tropics, for example, the escarpment and highland rainforest communities remain largely intact, whereas the coastal lowland and tableland rainforest communities have been severely depleted. Of 24 endangered Wet Tropics regional ecosystems, 18 occur on the coastal lowlands as fragmented remnants while a further five are from basalt landscapes on the Atherton Tableland (Goosem et al. 1999). The status of endangered, in general, refers to those regional ecosystems that have been reduced to less than 10% of their pre-European extent (Sattler and Williams 1999). Rainforests are remnants of the oldest types of vegetation in Australia. Many species have ancestors dating back to the Cretaceous or early Tertiary Period, over 65 million years ago (Commonwealth of Australia 1986; DASETT 1987; BRS 2003). For this reason, Australian rainforests have major historical and scientific significance. Australian rainforests are more important for the maintenance of biodiversity than their small area would imply. Five of the 13 centres of plant diversity identified in Australia are dominated by rainforest, while a further three have rainforest components (BRS 2003).

17.2.1 The Wet Tropics Rainforests

The Wet Tropics rainforests in Australia occurs as a narrow strip along the East coast from 15°30′S to almost 19°25′S and covers approximately two million hectares. Such is the biological significance of the region that a large part of this was inscribed on the World Heritage List on 9th December, 1988, as the Wet Tropics of Queensland World Heritage Area (WTWHA). The listing was the direct consequence of the accumulated scientific research and understanding of the region's rainforests until that time (see McDonald and Lane 2000). The tenure of the land within the World Heritage Area (WHA) is complex and changing (Table 17.2). There has been a progressive conversion of land tenures within the WTWHA to national park [e.g. from 14% at time of listing (IUCN 1988) to 64% in 2007] and a progressive reduction in the area of various lease tenures.

Queensland's Wet Tropics itself is a mega-diverse region and is represented on *The Global 200* list (Olson et al. 2000), which is a collection of the Earth's 200 most outstanding, important and diverse terrestrial, freshwater and marine habitats. Although representing only 0.013% of the earth's land surface (Geoscience Australia 2009), the Wet Tropics, for its size, makes a significant contribution

Table 17.2 The changing nature of land tenure in the Wet Tropics of Queensland World Heritage Area (WTWHA)

	Percentage of WTWHA			
Tenure	1995	2000	2006	2007
National park	28	32	63.9	64.3
Forest reserve	–	–	8.2	5.1
State forest	38	39	0.2	3.4
Timber reserve	8	8	7.8	7.8
Various reserves and dams	1	1	1.1	1.1
Unallocated state land	7	7	6.4	6.4
Leasehold[a]	15	10	9.3	8.9
Freehold and similar	2	2	1.9	1.9
Others (rivers, roads, esplanades, etc.)	1	1	1.2	1.2
Total	100	100	100	100

[a] Leasehold includes leases over a variety of base tenures including National Park, Timber Reserve, Forest Reserve and State Forest – where a lease has been issued over a base tenure, the area of the lease has been subtracted from the base tenure

Table 17.3 Proportion of Australia's species found in the Wet Tropics

Plants	%	Animals	%
Ferns	65	Marsupials	30
Cycads	21	Bats	58
Conifers	37	Rodents	25
Orchids	30	Birds	40
Vascular plants	26	Frogs	29
		Reptiles	20
		Freshwater fish	42

to global biodiversity. The high level of regional endemism increases this relative contribution with vascular plants contributing 1.7% of the world total, mammals 2.5%, birds 3.4% and amphibians 1.1%. The Wet Tropics contains the richest variety of animals and plants in the country, including two-thirds of the butterfly species, half of the birds and a third of the mammals (Table 17.3). A very high proportion of the fauna and flora is endemic to the Wet Tropics (Commonwealth of Australia 1986) and includes 70 vertebrate species. More than 400 plant and 76 animal species are officially listed as rare, vulnerable or endangered (WTMA 1999). The Wet Tropics also provides an unparalleled living record of the ecological and evolutionary processes that shaped the flora and fauna of Australia over the past 400 million years when it was first part of the Pangaean landmass and then, later, the ancient Gondwana continent. For example, the rainforests of the Wet Tropics have more plant taxa with primitive characteristics than any other area on Earth. Metcalfe and Ford (2009) calculate that the Wet Tropics flora (both rainforest and non-rainforest habitats of the bioregion) contain 4,035 spp. in 1,369 genera in an area of 20,000 km^2, which compares favourably with that of New Caledonia (2,422 spp., 19,000 km^2) and Costa Rica (5,250 spp., 51,000 km^2). Based on a modern phylogeny, they calculate that of the 28 near-basal angiosperm lineages, 16 have representatives extant in the bioregion. This is similar for the floras of New Caledonia and Costa Rica. One primitive family, Austrobaileyaceae, is found only in the Wet Tropics.

The Wet Tropics bioregion covers approximately two million hectares and includes the entire WTWHA (894,420 ha). Although the rainforests of Queensland's Wet Tropics are small in size compared to the rainforests of other parts of the world, the WHA covers such a high proportion of the rainforested area that it ranks high in size amongst other rainforest WHA (Table 17.4).

Until the 1970s, it was thought that rainforests were "alien" to the Australian landscape, while sclerophyll types of vegetation, such as eucalypts and acacias, were considered quintessentially Australian. Rainforests were considered to be recent invaders across the land bridge that, in fairly recent geological times, connected Australia with New Guinea. Ecological, biogeographical and taxonomic research, however, gradually provided evidence that radically changed this view (Webb 1959; Webb and Tracey 1981; Webb et al. 1976, 1984). It was not just that rainforests had evidently adapted themselves to various climatic conditions (tropical, monsoonal, sub-tropical and temperate) which bore witness to longer local

Table 17.4 Size comparisons of world heritage tropical rainforest properties

Major rainforest type	Country	Size (ha)
Lowland rainforest		
Salonga National Park	Zaire	3,600,000
Lorentz	Indonesia	2,500,000
Okapi Faunal Reserve	Zaire	1,372,625
Wet Tropics of Queensland	Australia	894,420
Virunga National Park	Zaire	790,000
Thungyai-Huai Kha Khaeng	Thailand	622,200
Kahuzi-Biega National Park	Zaire	600,000
Sian Ka'an	Mexico	528,000
Dja Faunal Reserve	Cameroon	526,000
Rio Platano Biosphere Reserve	Honduras	500,000
Tai National Park	Cote d'Ivoire	330,000
Ujung Kulon National Park	Indonesia	78,359
Los Katios National Park	Colombia	72,000
Tikai National Park	Guatemala	57,600
Sinharaja Forest Reserve	Sri Lanka	8,864
Montane rainforest		
Canaima National Park	Venezuela	3,000,000
Talamanca/Amistad	Costa Rica/Panama	791,592
Sangay National Park	Equador	271,925
Machu Picchu	Peru	32,592
Mount Nimba Reserves	Cote d'Ivoire	18,000
Mome Trois Pitons	Dominica	6,857
Sub-montane rainforest		
Manu National Park	Peru	1,532,806

habitation than was commonly believed. It was other irrefutable evidence, such as the discovery of many families of primitive ancient angiosperms in the Wet Tropics, that confirmed these rainforest ecosystems as among the oldest rainforests on Earth. Although many of these elements also occur in New Caledonia and to a smaller extent in New Guinea, the Wet Tropics also displays a co-evolution with related sclerophyll floras and faunas.

The varied topography of the Wet Tropics and its effect on rainfall is the reason behind the region's high biodiversity. A combination of high elevated mountains and plateaus that run roughly perpendicular to the prevailing south-east trade winds results in the Wet Tropics being the wettest region in Australia (Turton et al. 1999). About one-third of the Wet Tropics bioregion is greater than 600 m above sea level, giving rise to cooler meso-thermal climates, in which annual average temperatures are below 22°C. Some plant and animal species are adapted to these cooler climates that occur in largely contiguous areas of higher altitude rainforest and it is these species in particular that are severely threatened by climate change (Williams et al. 2003) as less than 5% of the total protected area is higher than 1,000 m above sea level. Approximately, 10% of the vertebrate species are endemic to the uplands and many of these would be highly threatened by rising temperatures. One of the remarkable features of the Wet Tropics is the sharp rainfall gradient from east to west, whereby across the eastern lowlands, rainfall may be 2,500–4,000 mm/annum, while in places across the montane region, rainfall may be as high as 16,000 mm/annum, with the western savanna region experiencing annual rainfall as low as 1,500 mm/annum. All these sharp changes can occur over distances of less than 40 km.

17.2.2 History of Human Settlement

Australia has a long history of settlement and use by Aboriginal people. Although there is a degree of uncertainty and controversy regarding when Aboriginal people arrived in Australia from Southeast Asia, a time frame of between 40–60,000 years before present is now generally accepted (Flannery 1995). All parts of Australia were occupied by these Aboriginal people, often referred to as Traditional Owners, and most were displaced or killed by European settlement. In the Wet Tropics region, there are currently at least 20 tribal groups and many of these people were displaced from their country when Europeans settled in the region in the late 1800s (Pannell 2008). To rainforest Aboriginal people or "Bama", the Wet Tropics is a living cultural landscape. This means that natural features are interwoven with rainforest Aboriginal people's religion, spirituality and economic use (including food, medicines and tools), as well as their social and moral organisation. The landscape identifies rainforest Aboriginal peoples' place within their country and reinforces their ongoing customary laws and connection to country. The country is therefore embedded with enormous meaning and significance to its Traditional Owners.

Early European settlers first cleared lowland rainforest to grow food for the local European population, but soon started to clear forest for timber. Elsewhere, Stork et al. (in review) discuss how human perceptions of rainforest values in the Wet Tropics have changed over time and how these changing value systems historically have influenced decisions concerning management of the environment. Such decisions are ultimately based on community values held at the time which also largely influenced the prevailing political climate at the local, national and often international level. For example, rainforests in the Wet Tropics, in the late 1880s and early 1900s, were viewed as fertile soil deemed more valuable if converted to pasture or crop lands. Even up to the late 1950s, land holders could not receive government incentive funding until the land had been cleared of trees. Between the 1930s and the 1960s, the perceived value of rainforests shifted towards timber resources and rainforests were retained as Crown Land in State Forests for the purpose of timber production. In the late 1970s and 1980s, the perceived values shifted again from a strictly utilitarian view as leisure time increased for Australians and international tourism started growing (Pearce 2008). Since World Heritage listing, the perception has progressively changed to emphasise the non-market values of rainforests – scientific, cultural and aesthetic (Stork et al. in review).

The first comprehensive European exploration of the wet tropical coast was the 1873 Dalrymple expedition whose primary purpose was discovery of agricultural lands, especially those suitable for sugar cane and other tropical crops. North of Mission Beach, Dalrymple (1874, pp. 615–617) reported on a "great coast basin" – densely forested and with half a million acres of soil "unsurpassed by any in the world – all fitted for tropical agriculture" and referred to this region as the "Northern Eldorado". This view that rainforest was of little worth and was an impediment to agriculture was clearly expressed by one "gentleman" after a visit to Lake Eacham on the Atherton Tableland: "Most of your readers know Atherton, and I look on this small settlement as marking the first skirmish in the coming war between the pioneers of civilization and the vast wilderness that stretches N S and E over hundreds of square miles. This war between man and the scrub has begun – and will never cease till the axe has laid the enemy low and smiling pastures have taken the place of the heavy scrub..." (Herberton Advertiser 2 August 1889).

For a long period, this narrow utilitarian perception of rainforest remained dominant and politicians, public servants and local promoters proposed huge schemes to develop most of the north Queensland "scrub lands" into small family farms (Frawley 1983). The Queensland Forestry Department argued determinedly against this proposed land alienation and for the reservation of forest lands for timber production, as well as for some national parks. The foresters were arguing for professional management of the forests for production forestry purposes, consistent with the utilitarian conservation philosophy of the "wise use" of resources. During the same period, major land clearing was being undertaken on the coastal plain and on the gentle terrain of the fertile Atherton Tableland, which generated conflict between those who valued rainforests as agricultural and pastoral land to be cleared as extensively and quickly as possible and those who valued rainforests for their longer-term timber resource. State economic prosperity was closely identified with rural development, and closer settlement became the accepted political objective. Growth of the dairying industry after 1890 was a major driver of landscape change in the region, expanding rapidly into rainforested areas with their supposedly fertile soils (especially basalt landscapes on the tablelands and well drained, alluvial landscapes on the coastal lowlands). In pursuit of this policy of the Government of that time, rainforest clearing proceeded without any assessment of its suitability. This policy of closer settlement and free-holding of crown land continued until the late 1950s with the post-World War II soldier settlement schemes.

The post-1960 period was very significant in the history of rainforest management, planning and utilisation for two reasons. First, the expansion in effort and expenditure by the Government into long-term management planning through the establishment of the Department of Forestry in 1959 with responsibilities for the reservation and management of national parks and the creation of a separate National Parks and Wildlife Service in 1975; second, the evolution of the conservation movement which successfully challenged the pre-1960 management models in favour of rainforest preservation and strict rainforest conservation models (Valentine and Hill 2008). This radical change in the way society values the region's rainforests was due in large measure to the changes in our knowledge and appreciation of the international scientific significance of the rainforests resulting from research (culminating in World Heritage inscription in 1988). This conflict in social and political values continued until as recently as the 1960s when the last large-scale clear-felling of forests (42,900 ha) for pastoral purposes occurred in the Tully River lowlands (King Ranch).

17.2.3 Recent Change in Perceptions of Rainforests

The Wet Tropics occupied a central position in Australian environmental politics throughout the 1980s. The events surrounding the World Heritage listing of the Wet Tropics were beset in controversy, characterised by protest campaigns for and against rainforest logging, including a political battle between the Queensland and Australian governments (Valentine and Hill 2008). There was a conflict between the then Queensland Government which supported logging of the rainforests and the Australian Federal Government which proposed to nominate the Wet Tropics for the World Heritage List. All local governments (Shire Councils) and the major representatives of rainforest Aboriginal people (Bama) in the region also opposed the listing.

New research and understanding regarding the origin and evolution of Australia's rainforests and events such as the second World Wilderness Congress held in Cairns in 1980 drew national and international attention to the significance of the rainforests of the Wet Tropics of Queensland and the threats to their internationally significant values. In the early 1980s, strong pressure was being mounted by conservation groups to protect the rainforests from logging operations. The primary focus of early campaigns was confined to the northern, "Greater Daintree" section of the region. In 1982, the Wet Tropics was included on The World Conservation Union's (IUCN) 1982 list of places deserving World Heritage protection. This provided the impetus for World Heritage listing of the Wet Tropics. A significant event in the campaign for rainforest protection came in November 1983 when a developer, supported by the Queensland Government, constructed a road through the lower Daintree rainforests (the Cape Tribulation – Bloomfield Road). This resulted in a blockade by protestors, which although unsuccessful in stopping the construction of the road, focused significant national and international attention on the area. In 1984, the Australian Heritage Commission engaged the Rainforest Conservation Society of Queensland to evaluate the international conservation significance of the area between Townsville and Cooktown. Their report concluded that *the Wet Tropics region of North-East Queensland is one of the most significant regional ecosystems in the world. It is of outstanding scientific importance and natural beauty and adequately fulfils all four of the criteria defined by the World Heritage Convention for inclusion in the* "World Heritage List" (Australian Heritage Commission 1987).

At the 12th Session of the World Heritage Committee meeting in Brasilia, Queensland's Wet Tropics nomination was endorsed and the area was officially inscribed on the World Heritage list on 9th December, 1988. In response to the heritage listing, the Commonwealth Government provided a AUD$75.3 million Wet Tropics of Queensland Structural Adjustment Package (SAP) for job creation, labour redeployment and assistance and business compensation to offset the impacts of the cessation of logging in the area.

17.3 Existing and Emerging Threats

Rainforests throughout the world, including the Australian rainforests, are highly contested landscapes as governments and the commercial sector seek to increase economic benefits from what are seen as largely unproductive forests. Globally, the major threats to rainforests include logging, both legal and illegal clearing, fire and general encroachment through increased road and rail access, invasive organisms, hunting and climate change (Laurance and Peres 2006). Laurance et al. (2001) highlighted the fate of tropical rainforests when they showed how the Amazonian rainforest might be reduced to 40% of their current coverage if proposed infrastructure projects were to come to fruition in Brazil. Earlier, Myers (1993) brought to the attention of the world the decline in rainforests (and tropical dry forests) due to the actions of growing numbers of shifting cultivators who were taking advantage of new access roads into previously inaccessible areas. Population growth is seen by many as a major threat to tropical forests and the extinction of tropical forest species (but see Wright and Muller-Landau 2006). In many parts of the world, and in particular in African rainforests, the bushmeat trade is devastating the mega-fauna of rainforests (Bennett and Robinson 2000). The loss of these large vertebrates will result in many changes to the structure and composition of tropical rainforests. These changes may well be exacerbated by the impact of climate change.

In Australia's Wet Tropics, logging and hunting are no longer major concerns, but other threats are now increasingly of importance and include internal fragmentation and human settlement infrastructure, climate change, the introduction and spread of weeds, feral animals and pathogens and alterations to fire regimes, water quality and quantity flowing into the Great Barrier Reef lagoon, flow regimes and drainage patterns (WTMA 2004; Laurance and Goosem 2008; Balston 2008; Goosem 2008; Congdon and Harrison 2008; Pearson and Stork 2008). Figure 17.2 (after Stork 2005) shows examples of human activities associated with pressures at a range of scales in regard to the Wet Tropics WHA. Environmental change is brought about by a number of factors that drive, influence and direct environmental issues. These drivers arise mainly from socio-economic activities and create the demand for resource use, access and community infrastructure that result in activities that place pressure on the natural values of the WTWHA. Most of these processes are strongly influenced by regional development demands, land use and land tenure patterns. The drivers, although originating outside of the WTWHA itself, result in activities or processes either within or outside the WTWHA, with the potential to adversely affect the condition of its natural values. Some processes,

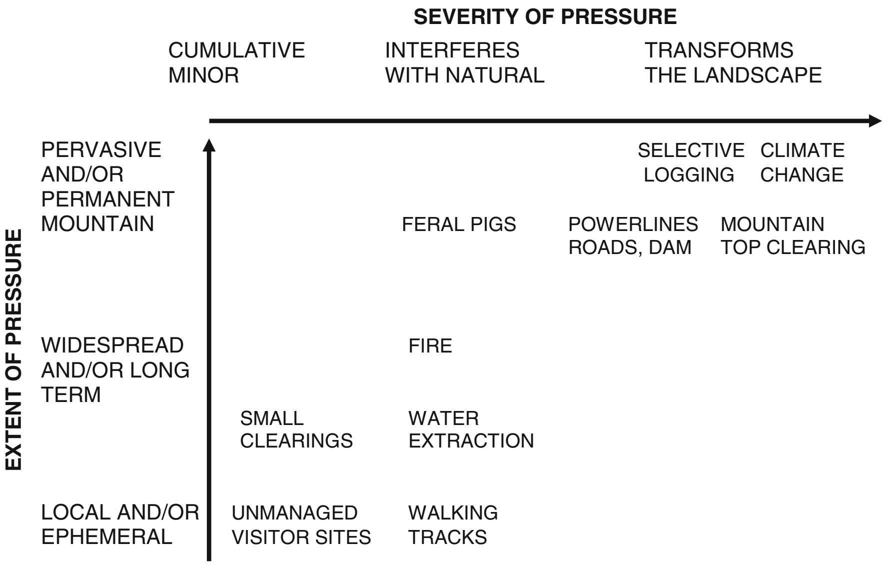

Fig. 17.2 Examples of human pressures on the Wet Tropics WHA at a range of spatial scales (after Stork 2005)

such as climate change, are likely to result in long-term and pervasive transformation of the Wet Tropics landscape, while others such as walking tracks will cause mostly local but cumulative minor impacts. Many of the ongoing threats are intermediate to the above and are undoubtedly interfering with natural processes with widespread and/or long-term consequences (Fig. 17.3 after Stork 2005). At the same time, declining water quality associated with agricultural and urban run-off resulting from poor land management is a major threat to the ecological and economic sustainability of the Great Barrier Reef WHA that in part borders the Wet Tropics WHA (Pearson and Stork 2008).

17.3.1 Timber Harvesting and Clearing for Agriculture

Human impact in the Wet Tropics bioregion is relatively low compared to other global tropical forest regions, with a large proportion of the region's forest cover originally present at the time of first European settlement remaining. The majority of the region's lowland and basalt tableland forest cover, however, has been cleared for agricultural purposes and large parts of the WTWHA have been affected by logging (IUCN 1988). Long-term average timber yields from what is now the WTWHA prior to its inscription in 1988 were 63,000 m^3/annum from a productive area of 158,000 ha. Up until listing, therefore, parts of the WTWHA had been available to a 70-year history of logging of varying intensity. Nevertheless, much of

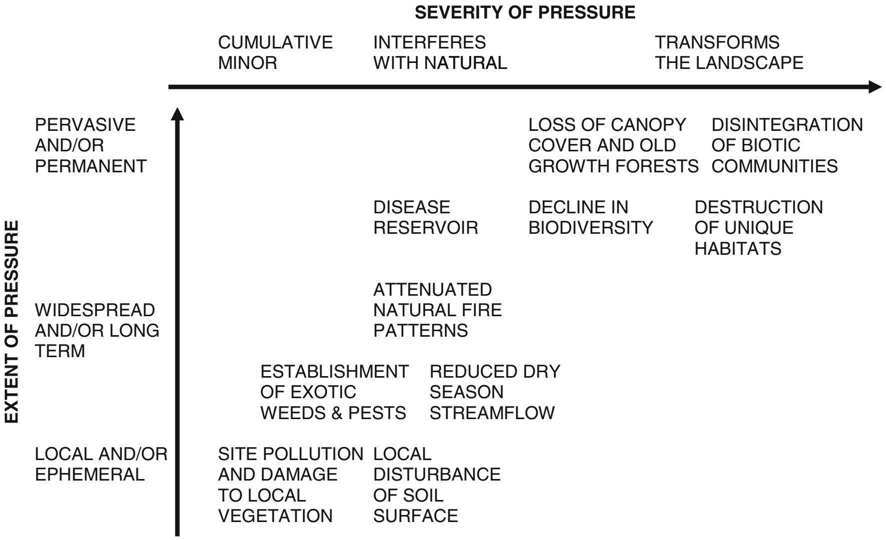

Fig. 17.3 Examples of consequence of human pressures on the Wet Tropics WHA at a range of spatial scales (after Stork 2005)

the WTWHA is in an undisturbed condition, having been inaccessible to logging (IUCN 1988) or other modern human use. Logging has been a prohibited activity in the WTWHA since 1987 and infrastructure associated with this industry has been phased-out, including the closing of over 6,500 km of no longer used, needed or serviceable unformed logging tracks which contributed to approximately 2,070 ha of clearing. However, some of these decommissioned roads now form the basis of walking tracks, such as the long-distance Misty Mountains Trails. There have been no clearings associated with new power line or new road construction within the WTWHA since listing.

17.3.2 Population Growth and Increasing Economic Development

Queensland's Wet Tropics bioregion is an increasingly desirable place to live, visit and invest in. As a result, human activity is increasing, which in turn places increasing pressures on the environment. Table 17.5 summarises the main socio-economic characteristics of the Wet Tropics Natural Resource Management (NRM) region that represents about 80% of the bioregion. While the Wet Tropics NRM region only covers 1% of Queensland, it contributes 10% and 23% of its agricultural and tourism activity, respectively (Stork et al. 2008). Over the last decade, population growth rates have been among the highest in the state outside the

Table 17.5 Wet Tropics natural resource management region statistics

Land area	2.2 million ha
Current population	220,000 people
Projected population growth by 2025	300,000 people
Land area under cropping	130,000 ha
Land under horticulture	47,000 ha
Land under improved pasture	65,000 ha
Land under grazing	600,000 ha
Total value of tourism industry	$2 billion
Number of visitors to region per year	3 million
Tourism sector employment	20% of regional total

Source: McDonald and Weston (2004)

south-east corner, with this adding to increasing pressure for resource use that has resulted in environmental degradation particularly along the coastal plain.

The main environmental impacts of sustained population growth in the Wet Tropics include those associated with (1) infrastructure development, such as the creation of new resorts and tourist attractions; (2) linear infrastructure developments, such as roads and walking tracks needed to transport tourists and residents in the region or power lines and waterlines to provide power and water (Goosem and Turton 2000; Goosem 2004; Turton 2005); (3) urban and peri-urban growth, particularly population increases in the areas adjacent to the Wet Tropics WHA; (4) water supply and increasing demand for more water storage and (5) waste disposal in environmentally sensitive areas.

Many of the regional-scale processes are interrelated, with the growth in tourism and associated service industries being the principal driver for all of them. Tourism and recreation activities and their associated environmental impacts on the Wet Tropics WHA have been largely associated with visitor use of walking tracks and trails, old forestry roads and tracks, day use areas, camping areas as well as water holes and rivers and maintenance of access infrastructure (Turton 2005). In addition to the fragmentation and isolation of rainforest patches resulting from broadscale agricultural land uses, there is also the impact of past internal fragmentation of the main rainforest blocks due to the network of linear infrastructure, including over 300 km of powerline clearings and 1,220 km of maintained roads (WTMA 2000). These extend through the rainforest and act as effective barriers to the movement of many rainforest species while providing a conduit for pest and fire intrusion into rainforest areas. Vehicular roads and tracks produce a multitude of biophysical impacts on rainforest ecosystems, including linear barrier effects on arboreal and ground-dwelling fauna, road kill and biotic and abiotic edge effects, which may extend more than 200 m into the adjacent forest (Goosem 2004, 2008). Other environmental effects include provision of alien habitat along road verges that are often colonised by non-rainforest fauna and flora, feral animals and weed species (Goosem 2004, 2008). They can also act as conduits for feral animals, weeds and soil pathogens, facilitating their movement and colonisation of core rainforest habitat (Goosem and Turton 2000). Rainforest roads disrupt canopy cover, leading to increased rates of erosion and sedimentation (Goosem and Turton 1998).

Linear clearings created by roads also create significant barriers to the movement of many rainforest animals, leading to sub-division of animal populations and associated demographic and genetic problems for many rare and threatened species (Goosem 2004).

17.3.3 Invasive Species and Diseases

The region is considered particularly vulnerable to the threat of invasive pest species. Werren (2001) identified 508 naturalised plant species in the region and the number of invasive plants has increased by almost 100 species/decade for the last 40 years (Fig. 17.4). A further seven mammal, five bird, five freshwater fish, two reptile and one amphibian species have also become naturalised (EPA 1999). Many environmental weeds affect large areas of rainforest or former rainforest lands that have been converted for agriculture. There are many feral vertebrates in the Wet Tropics including pigs, cats, dogs, cattle, deer, some bird species and numerous introduced fish. In an analysis of the risk posed by these feral animals, one species which has not yet been seen in the area, the fox, was identified as posing the greatest potential threat (Harrison and Congdon 2002; Congdon and Harrison 2008). Recently, another introduced species, the rabbit, has moved north into agricultural areas and it is expected that its main predator, the fox, will soon follow

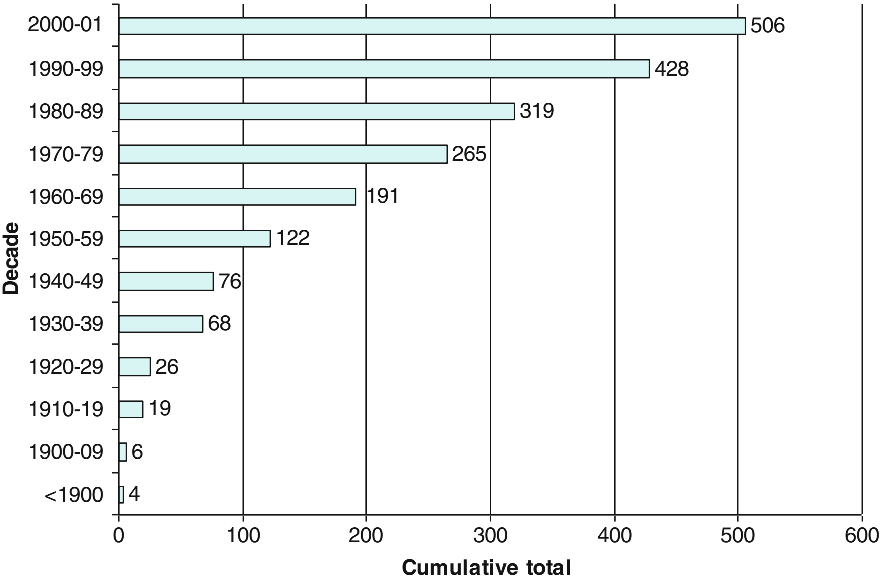

Fig. 17.4 The total number of naturalised plant species recorded in the Wet Tropics region by 10-year increments (after Werren 2001)

and will present a major threat to many native vertebrates. Cane toads introduced from Hawaii are now very widespread.

The problem of pest species is likely to increase for the WHA with the globalisation of trade and the demand for access to more areas of rainforest sought by the tourism industry. The spread of soil pathogens by hikers along walking trails and by vehicle tyres on forestry roads is a potentially serious threat. Of particular concern is the spread or activation of the root rotting fungus, *Phytophthora cinnamomi*, which is known to cause forest dieback (Worboys and Gadek 2004). Such fungal dieback has been identified from 190 sites (Gadek et al. 2001). Rainforests on acid igneous rocks at altitudes above 750 m are particularly susceptible to this pathogen, suggesting that 14% of the region's remaining rainforests may be susceptible to virulent dieback outbreaks. Research has shown a strong association between distributions of *P. cinnamomi* in mapped dieback polygons and the location of roads and old forestry tracks in the area (Gadek and Worboys 2002). Recreational use of long-distance walking tracks by hikers and old logging tracks by off-road enthusiasts has the potential to spread or activate the fungus spores to susceptible areas currently unaffected by dieback. But one unknown factor is whether this disease can be spread by native and introduced fauna such as cassowaries and feral pigs.

17.3.4 Climate Change

The forests of the WTWHA owe their genesis and past and present distributions to long-term cycles of change in climate. It may seem ironic, then, that climate change is now regarded as the single biggest threat to their future.

Wet Tropics researchers have been global leaders in the field of climate change impacts on tropical rainforests and their biota (Krockenberger et al. 2004; Williams and Hilbert 2006). Research shows that the biodiversity of the WTWHA may be highly sensitive to climate change (Balston 2008; Williams et al. 2003; Williams and Hilbert 2006). The location and extent of rainforests, in particular, are largely determined by rainfall and its seasonality, while the type of rainforest and many of the organisms found within them depend upon narrow temperature ranges. Climate change impacts upon biodiversity either directly per se or indirectly through interactions with other species that are affected by climate change, which leads to changes in competition, food, habitat and predation patterns and processes. For some species, these indirect impacts may be stronger than direct impacts. This cascade of climate change impacts also interacts with other human pressures on biodiversity such as habitat degradation and loss, water extraction and regulation of flow regimes, pollution and introduction and spread of pest species. Climate change impacts not only add to these other pressures but also interact, altering the way species and ecosystems would otherwise respond and adapt.

Biological impacts of climate change include the direct changes to organisms, such as physiological and behavioural changes, including differential responses by different species in both magnitude and type to changing conditions, and changes in timing of species' life-cycles (phenology). Changes will also occur to the composition, structure, function and services of ecosystems, including changes in nutrient cycling and natural resource supply (e.g. water) and changes in predator–prey, parasite–host, plant–pollinator and plant–disperser relationships in the Wet Tropics WHA and surrounding landscapes (Krockenberger et al. 2004; Williams and Hilbert 2006). Balston (2008) summarises the current climate of Cairns and what we might expect by 2030 and 2070 as a consequence of climate change. The Wet Tropics region may expect a 1°C warming by 2030 and as much as 2°C by 2070, together with more hot days with maximums over 35°C. Rainfall is predicted to decline by as much as 10%, with more pronounced dry seasons and higher interannual variability. Evaporation is expected to increase in response to higher average temperatures and slightly lower rainfall. Greatest impacts of climate change are likely to be in the upland forest (above 600 m elevation), where cool-adapted species are found. Modelling studies by Hilbert et al. (2001) have shown that these upland forests are particularly sensitive to changes in temperature and rainfall. Changes as small as a 1°C increase in temperature and a 10% decline in rainfall may result in a significant contraction of rainforest above 600 m in elevation, resulting in less suitable conditions and more fragmented rainforest habitat. Problems are exacerbated by the fact that many regionally restricted (endemic) species occur in the Wet Tropics within extremely narrow climatic ranges. Particularly alarming is the modelling work by Williams et al. (2003) which shows that high elevation species may become progressively more restricted as their already confined climatic habitat range declines or even disappears under global warming. Much of this modelling work formed the basis of a controversial global review (Thomas et al. 2004) that showed that about one-third of all the world's species are threatened with extinction within 50 years due to global warming, with many endemic species from far north Queensland likely to face an even higher loss.

Ecological impacts include changes in the location of native species' habitats, resulting in range shifts and/or losses due to range expansions, contractions and eliminations. In addition, there may be changes in breeding, establishment, growth, competition and mortality. There will also be increased opportunity for range expansion of invasive pest species including weeds, feral animals, pathogens and parasites. Range expansion opportunities also exist for some native species. As a consequence, we can expect changes in the structure and composition of ecological communities, and formation of novel communities based on new species assemblages. Ecosystem function is also likely to be severely altered by climate change in far north Queensland (cf. Krockenberger et al. 2004; Crimp et al. 2004). In particular, ecosystem services provided by our rainforests, such as carbon storage and water supply, are predicted to change over the next 50–100 years. At present, our cool upland forests contain a large storage "pool" of carbon compared with the warmer lowlands where there is a much higher turnover of biomass (D. Hilbert, personal communication). Under global warming scenarios, there is a real risk that much of this carbon will be released into the atmosphere, thereby enhancing anthropogenic emissions of greenhouse gases. Our upland rainforests also act as "cloud strippers", with field studies showing that up to 30% extra water is delivered to Wet Tropics catchments from this process (McJannet et al. 2008). Under global warming, the cloud-base will increase about 100 m for every 1°C in temperature, thus reducing water input to our catchments, particularly in the dry season.

Population impacts refer to the ultimate impact on species in terms of changes in their abundance and distribution. Population impacts include changes in presence/absence and relative/absolute abundances and differential individual species' responses to warmer and drier/moister conditions. Individual species responses may result in increased risk of extinction for species that are already vulnerable due to limited climatic ranges, limited dispersal ability, specialised habitat requirements, small populations and/or low genetic diversity. These individual species responses, in turn, may interact with other natural and artificial factors including changes in the intensity, frequency and seasonality of extreme events such as cyclones, floods, droughts and fires and changes in human land-use pressures (synergies with changes to land use and other population pressures on the environment).

17.4 Conclusions

1. The Australian Wet Tropics rainforests comprise a surprisingly important hotspot of biodiversity within the recently recognised Forests of East Australia biodiversity hotspot that covers a much larger area of Eastern Australia.
2. The declaration of world heritage status for a large part of these forests coupled with a ban of logging has provided a new conservation and management regime. However, new threats from invasive species, diseases and climate change may provide potentially much greater threats in the long term than the now banned logging. Economic development and population growth in areas surrounding the WHA, although providing new employment opportunities, also need to be well managed if these rainforests are to be protected in the long term.
3. Indigenous Australians, once largely removed from their native forest lands during early European settlement, are now more involved in the co-management of their traditional country.

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Chapter 18

Explosive Speciation and Adaptive Radiation of East African Cichlid Fishes

Christian Sturmbauer, Martin Husemann, and Patrick D. Danley

Abstract Cichlid fishes are the most species-rich group of all teleost fishes. Their diversity is centered in the East African Great Lakes where more than 2,000 species evolved within the past 10 million years, representing the fastest vertebrate radiation known. Ongoing molecular phylogenetic analyses indicate that the cichlid radiation originated within Lake Tanganyika. Within the Tanganyikan radiation, seven lineages diversified during the primary radiation to occupy all available freshwater fish niches. The Tanganyikan radiation is the oldest, containing the greatest phenotypic diversity of all East African cichlid radiations, and is ancestral to the cichlid radiations found within Lakes Victoria and Malawi. The radiations in Victoria and Malawi are reciprocally monophyletic and are rooted within the C-lineage of the primary Tanganyikan radiation. While greater numbers of species are found within both Lakes Victoria and Malawi relative to the Tanganyikan radiation, these species flocks have a lower phenotypic diversity relative to the older Tanganyikan radiation. The construction of phylogenetic hypotheses has allowed researchers to explore the extraordinary morphological and behavioral diversity within an evolutionary framework. As a result, the study of cichlids has begun to answer many fundamental questions about the driving forces, mechanisms, and pathways of diversification. These studies demonstrated that cichlid diversification has been influenced by a complex combination of micro-allopatry, natural and sexual selection, facilitated by genetic mechanisms. Here we discuss these patterns, processes, and influences and also point to specific biological conservation problems of cichlid species flocks due to their extreme species richness and restricted species distribution. The current threats are not (yet) caused

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by habitat destruction and pollution but by overharvesting. Possible tactics to maintain diversity are proposed.

18.1 Introduction

With about 25,000 species formally described, teleost fishes are the most species-rich group of vertebrates. Of these, more than 10% belong to a single family – the Cichlidae. Cichlids have diversified into all imaginable ecological niches in available tropical freshwater systems and stand out as a paradigm for explosive speciation and adaptive radiation. Their multitude of body shapes, specializations, colors, and behaviors is unsurpassed (Boulenger 1898; Fryer and Iles 1972; Greenwood 1973, 1974, 1984a; Barlow 2000; Chakrabarty 2005). Two hundred and twenty genera are currently recognized in FishBase (http://www.fishbase.org/). Their natural distribution spans the southern tip of India and Sri Lanka with three species, Madagascar with 47 taxa in five genera (http://www.cichlid-forum.com/articles/species_list_madagascar.php), Central- and South America with 400–500 species and Africa with probably over 2,500 species. Interestingly, cichlids have not colonized Australia. In accord with the sequence of the split of Gondwana, Indian and Malagasy cichlids form the most ancestral split in the diversification of cichlid fishes, followed by the split between the African and American lineages (Zardoya et al. 1996; Streelman et al. 1998; Farias et al. 1999, 2000; Sparks 2004). Few species managed to move northward into the North American subcontinent (New Mexico and Texas) and into Asia Minor and Asia (Jordan valley and Iran). The maximum evolutionary age of cichlids is thus constrained by vicariance to 130–165 million years and the split between African and American cichlids to about 70–90 million years (Chakrabarty 2004). While riverine ecosystems tend to be relatively species-poor (Katongo et al. 2005, 2007; Koblmüller et al. 2008a) – with the exception of the large South American rivers and perhaps the Zambezi (Joyce et al. 2005) – lakes comprise extremely species-rich communities. Their hotspot of biodiversity clearly lies in the three East African Great Lakes, Victoria, Malawi, and Tanganyika, where an estimate of 1,800–2,000 species, i.e., 60% of the total cichlid diversity, are centered in species flocks (Greenwood 1984a). With a surface area of 68,800 km^2, Lake Victoria is the largest lake on earth and contains an estimated number of >500 cichlid species (Seehausen 2002). Lake Victoria is not a rift lake and is relatively shallow with a maximum depth of about 80 m. Its maximum geological age has been gauged to be between 250,000 and 750,000 years (Johnson et al. 1996), while the actual age of the species assemblage is a matter of discussion as a dry-up of the lake 17,000–11,700 years ago might have terminated the species flock partially or as a whole (Johnson et al. 1996; Seehausen 2002; Fryer 2004). In terms of monophyly, molecular phylogenetic studies suggested the Lake Victoria haplochromines to be part of a larger phylogenetic lineage of modern haplochromines that are found in several water bodies surrounding the lake including Lakes Albert, Edward, George, Kyoga, and Kivu and their interconnecting rivers (Meyer et al. 1990; Nagl et al. 2000; Seehausen et al. 2003; Verheyen et al. 2003). Lakes Malawi and Tanganyika are true rift lakes, situated in the East African rift valley between the central and eastern African tectonic plates. Lake Malawi is about 700 m deep and has a tectonic age between 2 and 5 million years (Johnson and Ng'ang'a 1990), with a probable younger age for its species flock due to a late Pleistocene dry-up (Delvaux 1995). Moreover, it experienced two severe reductions in lake level during two East African mega-droughts 75,000 and 135,000 years ago (Owen et al. 1990; Scholz et al. 2007), so that several species of rock-dwelling cichlids may be extremely young (Genner et al. 2010). Overall, it contains 500–700 endemic cichlid species (Turner et al. 2001). With a maximum depth of 1,470 m, Lake Tanganyika is the deepest of the three lakes and also the oldest. Its geological age was estimated to be between 9 and 12 million years. Unlike Lake Malawi which consists of a single lake basin, Lake Tanganyika is made up of three basins. The current Lake Tanganyika is likely the product of the fusion of three proto-lakes to a single large lake during its long history (Cohen et al. 1993, 1997). Tanganyika's cichlid assemblage may be younger than the basin(s) themselves, but most likely of an age of 5–6 million years (Koblmüller et al. 2008b; but see Genner et al. 2007). Interestingly, with an estimated total number of 250 endemic species Lake Tanganyika has fewer species than Lakes Malawi and Victoria, albeit their overall degree of eco-morphological divergence is much greater (Greenwood 1984b).

18.2 Evolutionary History and Trajectories of Cichlid Fishes

18.2.1 Patterns of Species-Richness in Cichlid Lineages

Previous molecular phylogenetic work suggested reciprocal monophyly of the extant African and South American cichlid lineages (Streelman et al. 1998; Sides and Lydeard 2000), rejecting the morphology-based placement of the African genus *Heterochromis* at the base of the South American cichlids (Kullander 1998). Within Africa, several lineages diversified at an early stage, many of them being restricted to particular biogeographic regions. The tribe Tilapiini (>88 species) is one of the two large African cichlid taxonomic units defined on morphological grounds (Greenwood 1984b; Eccles and Trewavas 1989). However, the Tilapiini turned out to be a conglomerate of several lineages (Klett and Meyer 2002), scattered among the remaining ancestral splits. The haplochromine cichlids turned out to be (almost) monophyletic, with a highly intriguing evolutionary history. Thus, the diversification of the tilapiine cichlids coincided with that of other ancestral African lineages, predating the African rifting processes, while that of the haplochromine lineage coincided with and in fact was tied into the very first wave of adaptive radiation triggered by the rifting process in East Africa, in the proto-lake(s) of Lake Tanganyika.

The species inventories of rivers and lakes clearly suggest that large lakes are the centers of diversity, while riverine faunas are relatively species-poor and less dominated by cichlid fishes (Fryer and Iles 1972). Diversification in riverine environments seems to be driven by range expansion, colonization by river capture and subsequent geographic isolation, so that vicariant and geographic speciation best explains the modest diversity of riverine cichlids throughout the world (Joyce et al. 2005; Katongo et al. 2005, 2007), with the few exceptions mentioned above. Small lakes are often shallow and swampy with papyrus reeds surrounding them and mostly contain few species (see Fig. 18.4 in Salzburger and Meyer 2004). For example, the shallow Lake Kanyaboli, a satellite of Lake Victoria harbors just seven haplochromine and two tilapiine species, of which only one or two are endemic (Odhiambo et al. 2011). Mayr (1942) already observed that species number correlates with lake size rather than age and suggested that the much higher number of ecological niches and/or the higher potential for spatial separation due to long shoreline facilitates the intralacustrine allopatric speciation (see also Barluenga and Meyer 2004). The enormous diversity and impressive endemicity rates in large East African lakes suggest intralacustrine speciation as the most common mode of diversification. Seehausen (2006) counted 27 lacustrine cichlid radiations in Africa. In all these lakes, cichlid fish invariably form the most species-rich teleost lineage. Cichlids consistently out-compete other fish groups when colonizing a newly emerging lacustrine ecosystem and in doing so, the species flocks ecologically diversify and occupy a range of niches. For these reasons, cichlid fishes represent an excellent model system to study adaptive radiation: the process of extremely rapid species formation coupled with ecological, morphological, and behavioral diversification.

The theory of adaptive radiation requires two conditions to be met (1) the formation of a new habitat or a dramatic change of an already existing habitat and (2) the possession of a so-called key innovation, a set of traits allowing for rapid adaptation to novel niches. Thus, one feature or a certain set of features allows one group to outcompete the other taxa, thereby giving rise to an abundance of monophyletic species. In the case of East African lakes, several teleost groups had the same chance to colonize the newly emerged lakes: cyprinids, characins, mormyrids, various catfish, sardines, Nile perches, and spiny eels; but judging from endemicity rates, only cichlids underwent major diversification. Such that while Lake Tanganyika contains four endemic Nile perch species, six catfishes, six spiny eels, and two sardines, 90% of the fish in Lake Tanganyika are endemic cichlids. In the case of cichlid fishes, the key innovation may be a highly effective combination of factors. The first concerns trophic morphology; cichlids possess two sets of jaws, a characteristic shared with other labrid families (Liem 1973; Mabuchi et al. 2007). The oral jaws have specialized for food acquisition and manipulation. A hydrodynamic tongue then passes captured food items to the pharyngeal jaws (Liem 1991). The pharyngeal jaws are formed by parts of the gill arches, are connected to the neurocranium via the pharyngeal apophysis and process food in a wide variety of ways before swallowing. Both jaws have evolved to realize diverse foraging strategies: Cichlid oral jaws can catch fish, shrimp, or insects, browse filamentous algae from rocks, comb off unicellular algae and detritus from algal bio-mats, and even bite off fish scales from other cichlid species. Pharyngeal jaws can macerate food items, crush gastropod shells, slice off tissue or staple fish scales before swallowing. Allometric changes of these structures together with modifications of other body parts enable cichlids to efficiently adapt to novel food niches, without the need of de novo evolution of anatomical features (Stiassny 1991; Albertson et al. 1999; Clabaut et al. 2007).

The second outstanding feature of cichlids concerns their efficient brood care (Fryer and Iles 1972). Ancestral lineages are substrate breeders from which several groups branched off by independently shifting to various ways of mouthbrooding, i.e., incubating eggs and/or fry in the buccal cavity (Goodwin et al. 1998; Stiassny and Meyer 1999). Both breeding modes involve territorial behavior and facilitate raising the young in densely packed communities. Concerning species diversity, all East African lakes except for Lake Tanganyika exclusively comprise maternal mouthbrooders of the haplochromine cichlid lineage. Only Tanganyika contains a sub-flock of the substrate-breeding lamprologine lineage, together with a variety of lineages with various styles of mouthbrooding. This diversity is the result of the multiple independent evolution of mouthbrooding in the course of the Tanganyikan radiation, which seeded the most species-rich lineage, the haplochromines. The haplochromines appear to have left the Tanganyikan proto-lake at an early stage to colonize several other water bodies (Salzburger et al. 2002b, 2005; Verheyen et al. 2003; Clabaut et al. 2005; Koblmüller et al. 2008b).

18.2.2 The "Out of Tanganyika Hypothesis"

Lake Tanganyika is the second-oldest lake in the world and was the first major water body formed during the East African rifting process. It has a highly complex geological history (Scholz and Rosendahl 1988; Gasse et al. 1989; Tiercelin and Mondeguer 1991; Cohen et al. 1993, 1997; Lezzar et al. 1996; Scholz et al. 2003). Seven lineages of cichlids colonized the emerging Tanganyikan proto-lake(s) and seeded the so-called "primary lacustrine radiation" (Salzburger et al. 2002b; Fig. 18.1). Cumulative molecular phylogenetic evidence suggests that this diversification event coincided with the establishment of deep-water conditions in a clear lacustrine habitat about 5–6 million years ago (Tiercelin and Mondeguer 1991; Cohen et al. 1993, 1997). This timeframe suggests that the Tanganyika radiation did not happen at the earliest stage of lake formation, dated at 9–11 million years ago, when the rifting process slowed down the Proto-Malagarazi-Congo River to form a series of shallow and swampy proto-lakes, interconnected by a meandering river network (Sturmbauer 1998). While the vast majority of species was not formed in these early swampy proto-lakes, this period in the Tanganyikan radiation was likely important in the divergence of the seeding lineages.

The seven seeding lineages were the ancestors of the substrate-breeding predator *Boulengerochromis microlepis*, the genus *Hemibates*, and of the Bathybatini,

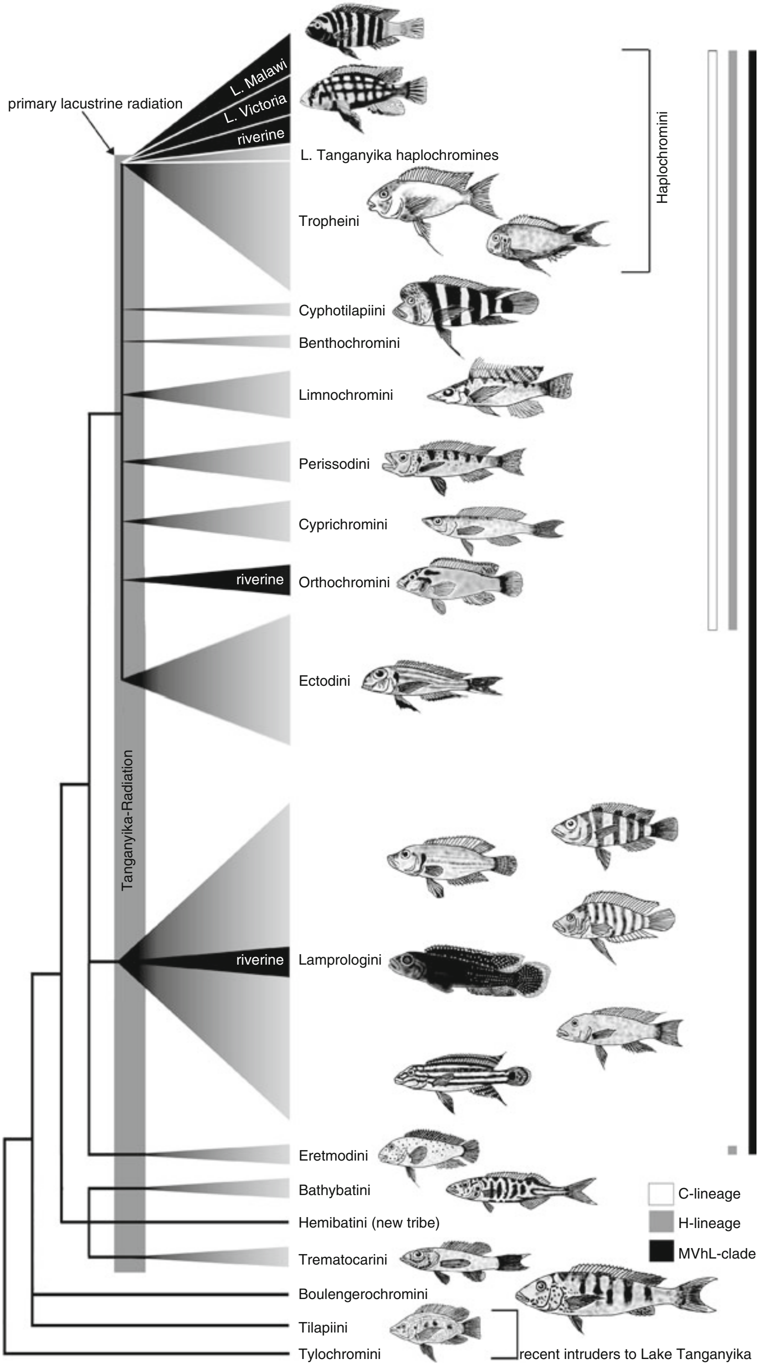

Fig. 18.1 Schematic molecular phylogenetic tree of the Lake Tanganyika cichlid species assemblage, and its relationships to the species flocks of Lakes Malawi and Tanganyika, based upon

Trematocarini, Eretmodini, Lamprologini, as well as of the C-lineage (sensu Clabaut et al. 2005). Molecular phylogenetic studies further demonstrated that *Oreochromis tanganicae* and *Tylochromis microlepis* had not yet been present in the lake at the time of the primary radiation, but had colonized the lake more recently (Klett and Meyer 2002; Koch et al. 2008). In the course of the “primary lacustrine radiation,” the substrate-breeding Lamprologini and the mouthbrooding C-lineage diversified rapidly into several new lineages (Salzburger et al. 2002b; Takahashi and Okada 2002; Terai et al. 2003; Clabaut et al. 2005; Sugawara et al. 2005). Mitochondrial DNA data suggest that haplochromine cichlids represent a paraphyletic assemblage, in that the *Orthochromis* species which are presently distributed in the Malagarazi River system, originated independently from the remaining haplochromines in the course of the “primary lacustrine radiation” (Salzburger et al. 2002b, 2005), but ancient incomplete lineage sorting may be an alternative explanation (Takahashi et al. 2001). Interestingly, the genus *Hemibates*, which was originally considered as a member of the Bathybatini, split from the ancestors of the large *Bathybates* species and the Trematocarini prior to the “primary lacustrine radiation” (Koblmüller et al. 2005).

Of the seeding lineages, two lineages, the Lamprologini and the C-lineage, underwent major diversification through successive divergence events. Both lineages gave rise to species that left the lake to colonize surrounding rivers (Salzburger et al. 2002b). Substrate-breeding lamprologine cichlids are found in the Lower Congo and the Malagarazi River, and haplochromine cichlids are found almost throughout Africa. In each of the newly colonized systems, both lineages further diversified.

The haplochromines consist of six lineages which originated within a short period of time, about 5.3–4.4 million years ago (Koblmüller et al. 2008b). They show a highly complex phylogeographic pattern, carrying the signature of climate- or geology-induced changes of the environment, with river capture due to tectonic tilting playing an important role for species dispersal across major drainage systems. The first lineage comprises only one species from southeastern Tanzania, *Haplochromis pectoralis*. The second lineage contains the eastern African genus

Fig. 18.1 (continued) combined evidence from several studies. Lineages that underwent radiation are indicated by triangles, whose size corresponds to the species number within these lineages (except for *triangles* symbolizing the riverine ancestors and the species flocks in Lake Malawi and Lake Victoria). *Black triangles* indicate lineages that do not occur in Lake Tanganyika. The “primary lacustrine radiation” (Salzburger et al. 2002b) is assumed to have coincided with the establishment of a true lacustrine tropical habitat with deepwater conditions about 5–6 million years ago. *Bars* to the *right* indicate taxonomic groups that have been proposed based upon combined mitochondrial and nuclear DNA data (C-lineage; Clabaut et al. 2005), allozyme data (H-lineage; Nishida 1991), and SINEs (MVhL-lineage; Takahashi et al. 2001). Note that the phylogenetic history of most tribes is much better resolved and that branch lengths and proportional times of radiation are not to be taken as accurate. Tribes are named according to Takahashi (2003) and Koblmüller et al. (2008b), with the exception for the suggested new tribe for *Ctenochromis benthicola* which turns out as close relative of the genus *Cyphotilapia* (Walter Salzburger, unpublished results)

Astatoreochromis with three species. The third lineage is represented by a single undescribed species, so far only found in the upper Lufubu River. The fourth lineage contains the genus *Pseudocrenilabrus* with a wide distribution all over eastern-, central-, and southern Africa. Lineage five represents the so-called modern haplochromines and lineage six, the *Serranochromis*-like cichlids, has its center of diversity in Central- and southern Africa. The modern haplochromines and the *Serranochromis*-like cichlids both have a wide and complementary distribution.

In terms of species richness, species flocks have been found in three clades: the *Pseudocrenilabrus* clade with a small species flock in Lake Mweru (Katongo and Seehausen, personal communication), the Serranochromines with a now riverine species flock that might have originated in Paleo-Lake Makgadikgadi (Joyce et al. 2005) or in another water body in this area (Frank Riedel, personal communication), and the modern haplochromines with maybe close to 2,000 species in about 25 lacustrine species flocks.

The endemic Lake Tanganyika tribe Tropheini is the sister group of the modern haplochromines. Their split from the remaining modern haplochromines was dated at 3.4 (3.0–4.0) million years ago. It is thought that the Tropheini originated in Lake Tanganyika, almost simultaneously with the remaining Tanganyikan mouthbrooding lineages, typical of lacustrine radiations but unusual for riverine assemblages (Joyce et al. 2005). However, it has been suggested that the riverine ancestor of the Tropheini re-entered Tanganyika and then subsequently radiated into several niches of predominantly rocky habitats (Salzburger et al. 2005).

The riverine haplochromines related to the Tropheini colonized Lakes Malawi and Victoria. At least one species of the Tropheini, *Ctenochromis hoorii*, also inhabits inflowing rivers and overlaps with *Astatotilapia burtoni*, the sister group of the Lake Victoria superflock. This sister group relationship is also supported geographically (Koblmüller et al. 2008b; Verheyen et al. 2003). Given that an undescribed modern haplochromine from the oasis El Fayoum in northern Egypt as well as *Haplochromis flavijosephi* from the Jordan Valley, nested within the East African clade (Werner and Mokady 2004), a Pleistocene dispersal along the Nile was suggested. Another lineage of modern haplochromines comprising the *Astatotilapia bloyeti* species complex colonized the more southern Tanzanian water bodies and seeded the Lake Malawi species flock. That said, it becomes evident that despite being independent radiations, the East African lacustrine haplochromines are connected by riverine species and root within the Lake Tanganyika Tropheini radiation.

18.2.3 Models of Adaptive Radiation

The tremendous diversity in East African lakes inspired the first evolutionary biologists who studied these systems to invoke novel modes of speciation involving sympatric mechanisms. The term scizotypic speciation was coined by Woltereck (1931) for Wallacean decapods and rapidly adopted to the cichlid speciation problem (Rensch 1933; Kosswig 1947; Brooks 1950). However, little progress was made towards a better understanding of the processes involved until the mid-eighties, as summarized by Ernst Mayr (1984). However, many issues plagued our understanding of the cichlid evolutionary history at that time: the age of the lakes and their species assemblages were unknown, taxonomic problems remained, and there was an almost complete lack of phylogenetic hypotheses. Nonetheless, three factors were recognized contributing to the extreme species richness of these systems: multiple colonization, fusion of several proto-lakes, and intralacustrine speciation (Mayr 1984).

Aside from geological processes, lake level fluctuations were recognized as an additional powerful promoter of intralacustrine allopatric speciation. Rossiter (1995) later termed this as "species pump speciation," in recognition that most cichlids are highly philopatric and restricted to particular types of shore substrate (Mayr 1984). Speciation was tied to the biological species concept of Mayr (1942, 1947) invoking the evolution of isolating mechanisms as barriers to gene flow that were thought to predominantly evolve in allopatric phases. Fine-scale geographic structure was recognized by Mayr as potential basis for microallopatric speciation. Speciation in connection to niche divergence, however, was questioned by him as being unlikely given the slight differences among incipient species. This opinion has changed in recent years and researchers now have a more differentiated view about the driving forces of speciation.

Speciation driven by (divergent) natural selection, termed ecological speciation, has been put forward as one major factor accounting for cichlid diversity (Schluter 1996; McKinnon et al. 2004). By comparing the overall degree of morphological divergence found within the three great East African lakes, Greenwood (1984b) concluded that species with similar morphologies would be characteristic in evolutionarily younger flocks, while highly diversified species would point to an older evolutionary age. These observations suggest that morphological diversification is driven by natural selection which continues to push morphologies towards more and more extreme forms (Mayr 1984). A second factor, sexual selection via mate choice, was brought up as a potentially powerful driving force (Dominey 1984), particularly in maternal mouthbrooders. Dominey's conceptual paper seeded a novel realm of research on sexual selection via female mate choice (Turner and Burrows 1995; Knight et al. 1998; Seehausen and Van Alphen 1999; Seehausen 2000). Moreover, the dominance of allopatric speciation was also questioned in particular phases of a radiation, and it was recognized that both natural and sexual selection have the potential to act in sympatric and allopatric situations (Sturmbauer 1998).

To reconstruct and understand the radiation pathways, knowledge of the geological and biogeographic history of the lake in question is needed to identify the probable source of seeding species. Then a phylogenetic hypothesis for the species flock is needed, based upon ecological, morphological, behavioral, and genetic data (Stepien and Kocher 1997). Finally, the modulators triggering speciation and eco-morphological diversification at each stage must be identified. Conceptual progress was made towards a better understanding of more large-scale patterns of the radiation process (Mayr 1984; Greenwood 1984b; Coulter 1991; Meyer 1993;

Schluter and McPhail 1993; Martens et al. 1994; Kornfield and Smith 2000; Schluter 2000; Turner 2007), and the stages of adaptive radiation progresses (Sturmbauer 1998; Danley and Kocher 2001; Streelman and Danley 2003). Radiations become adaptive by the tight coupling of fast speciation rates and eco-morphological and/or behavioral diversification. When natural selection is involved, speciation events show a "niche divergence first – speciation later" pattern, in turn, when sexual selection is the prime driving force, a "speciation first – divergence later" pattern emerges. The relative importance of the factors driving the whole process shifts with time; adaptive radiation must be viewed as an interactive process with a self-generated shift of abiotic and organismic modulators (Sturmbauer 1998).

The initial stage of cichlid adaptive radiation is characterized by riverine colonizers. Such species are generalists, able to cope with a seasonally fluctuating environment, and capable to colonize a variety of lake habitats still free from more specialized competitors. Accordingly, the first speciation events are tied to the colonization of major habitats such as rocks, sand bottom and the pelagic zone (Danley and Kocher 2001), so that the first emerging species adapt to "fundamental niches," possibly via sympatric mechanisms given the great dispersal ability of generalist colonizers (Sturmbauer 1998). Data from several systems suggest that this to be a common trend in vertebrate radiations (Streelman and Danley 2003). Lake Malawi, for example, was colonized by a generalized cichlid that first diverged into two major clades, the rock-dwelling mbuna and a sand-dwelling clade, plus several other oligotrophic lineages (Moran et al. 1994; Danley and Kocher 2001). The polyphyletic Lake Tanganyika radiation proceeded in a similar fashion, in that each diversifying lineage seems to have picked one habitat type and fundamental niche. Tilapiine cichlids in a West African crater lake (Schliewen et al. 1994, 2001; Schliewen and Klee 2004) and Heroine cichlids in the Central American Lake Apoyo (Barluenga et al. 2006) also follow the "major habitat first" rule.

The second phase of diversification results from the subdivision of fundamental niches. Within each fundamental niche, species emerge through the modification and refinement of the trophic apparatus. As a result, lineages which diverged during this phase can be distinguished based on trophic structures, feeding behavior, and diet. Such adaptations to the partitioned macrohabitat may further reduce gene flow thereby facilitating species divergence (Sturmbauer 1998). This pattern can be found in both Lake Malawi and Tanganyika cichlid lineages (Albertson et al. 1999; Sturmbauer and Meyer 1993; Sturmbauer et al. 2003; Salzburger et al. 2002b; Koblmüller et al. 2004, 2005, 2007a, b, c; Duftner et al. 2005; Brandstätter et al. 2005) and seems to be general for aquatic and terrestrial vertebrates (Streelman and Danley 2003).

A third phase of radiation promotes the divergence of reproductive characters without large eco-morphological change. During this phase, speciation seems to be primarily driven by sexual selection on male mating-relevant traits, such as male signaling phenotypes. This process is evident many species-rich radiations, such as the Victorian and Malawian haplochromine radiations, but is not wide spread in the relatively species poor Tangyanikan (Streelman and Danley 2003).

18.3 Factors Driving Divergence

18.3.1 (Micro-) Allopatry and Reduced Gene Flow

Geographic separation and extrinsically reduced gene flow are thought to be of primary importance in the majority of speciation events (Mayr 1942). In East African lacustrine cichlids, allopatric divergence is thought to have occurred through large lake level fluctuations, which split Lake Tangyanika into separate basins (Sturmbauer et al. 2001) and has isolated satellite lakes from the main lake basins of Lakes Malawi and Victoria (Brooks 1950; Greenwood 1965; Genner et al. 2007).

While the type of large-scale vicariance events common in other systems have played a role in the evolution of East African cichlids, the reduction of gene flow in these can occur over much shorter geographical scales and in the absence of major geologic events typically associated with divergence via vicariance. Many studies demonstrated between-population differentiation across as little as 2–5 km (Kornfield 1978; Van Oppen et al. 1997; Danley et al. 2000; Rico and Turner 2002; Smith and Kornfield 2002; Duftner et al. 2006; Koblmüller et al. 2007c; Sefc et al. 2007; Streelman et al. 2007; Wagner and McCune 2009). As a result, many East African cichlid species are “narrow endemics” often only present on a single stretch of continuous habitat (Ribbink et al. 1983). Furthermore, the shoreline of Lakes Malawi and Tanganyika consist of a patchwork of sandy and rocky habitats. This, and the extreme territoriality of most members of the Tropheini and Haplochromini, suggest that no large geographic distances or barriers are needed to reduce gene flow between populations living in neighboring habitat patches. The extreme philopatry, maternal mouthbrooding, and lack of dispersal during any life stage create circumstances in which microallopatric divergence can occur on the order of kilometers (Sturmbauer and Meyer 1992; Verheyen et al. 1996; Van Oppen et al. 1997; Arnegard et al. 1999; Markert et al. 1999; Danley et al. 2000; Salzburger et al. 2005). The low gene flow between neighboring populations suggests that even weakly differentiated selective environments could lead to the fixation of characters within local populations (Danley et al. 2000).

18.3.2 Localized Adaptation

The reduction of gene flow can lead to independent evolutionary trajectories. Different localities may comprise varying environmental conditions and selective pressures; these may involve factors such as rock size, inclination, wave exposure, food availability, and predation pressure. In addition, light environment, water turbidity, and other parameters influencing mate recognition may vary among sites and likely influence intensity and direction of sexual selection (Seehausen et al. 1997). Hence, local adaptation can be driven by natural as well as by sexual selection, and indeed, population differences have been found in trophic characters (e.g., Streelman et al. 2007; Herler et al. 2010) and mate choice traits (e.g., Maan et al. 2004).

18.3.3 Sexual Selection

Dominey (1984) was among the first to convincingly argue that sexual selection had a major influence on cichlid diversification. Since then sexual selection has been implicated in the divergence of a wide variety of phenotypes including brain size (Gonzales-Voyer et al. 2009), cooperative behavior (Bruintjes and Taborsky 2008), and territorial behavior (Markert and Arnegard 2007). Male nuptial coloration is the most widely studied target of sexual selection. The diversification in hue and color pattern is obvious and widespread particularly in the maternally mouthbrooding cichlids. Furthermore, diversity in color pattern is one of the most easily identified phenotypes by the human sensory system. However, recent evidence suggests that visual cues alone are not always sufficient for accurate mate discrimination. Mate recognition systems likely include visual, acoustic, and chemical characters. Recently, it has been suggested that selection on multiple cues might accelerate speciation rates, and different communication systems might act in close association with each other (Blais et al. 2009; Smith and Van Staaden 2009). Here, we review the different communication systems on which sexual selection may act and their impact on reproductive isolation and speciation.

18.3.3.1 Vision

Most research on communication in cichlids has concentrated on visual cues. This is easy to understand if one regards the great conspicuous diversity of male breeding coloration. Different aspects of morphology and coloration have been shown to ensure assortative mating and hence prevent hybridization (Seehausen et al. 1997; Seehausen and van Alphen 1998; Blais et al. 2009).

Body Size

Schliewen et al. (2001) found strong size-assortative mating in two sister species of cichlids in a lake in Cameroon. A study by Baldauf et al. (2009) revealed preferences for larger mates of both sexes in the West African cichlid *Pelvicachromis taeniatus*. Seehausen and van Alphen (1998) suggested that body size can be a mate choice signal when color is not available. Also, indirectly selection may act on body size. In some species, larger males are able to acquire larger or higher quality territories which are preferred by females (Markert and Arnegard 2007).

Color Pattern and Hue

East African cichlid fishes are well known for their amazing variety of color morphs. Typically, both males and females of a given species can be distinguished from sympatric species based on color pattern. However, female color patterns are generally dull and are believed to confer some degree of crypsis. In contrast, males, particularly those of the rock-dwelling cichlids, are conspicuously bright. Because male color pattern is so easily distinguished by the human sensory system, it is the most widely studied character believed to be under sexual selection.

Male nuptial coloration and female mate choice are known to contribute to assortative mating and reproductive isolation in many cichlid species (Couldrige and Alexander 2002; Jordan et al. 2003; Venesky et al. 2005). Stelkens and Seehausen (2009) found that phenotypic divergence, including nuptial coloration, is a better predictor for reproductive isolation than genetic distance for a closely related group of East African cichlids. Mate choice experiments using different light environments and field studies suggested that hue might be the most important cue used for mate evaluation (e.g., Seehausen et al. 1997; Seehausen and van Alphen 1998; van Oppen et al. 1998; Streelman et al. 2004; Maan et al. 2010). Other studies suggest that color pattern is the most important visual cue (e.g., Couldrige and Alexander 2002; Jordan et al. 2003; Stelkens et al. 2008). The final evaluation of each cue remains and present knowledge suggests that a combination of both color and hue might be decisive for mate choice.

While much work has been done to describe the role that color pattern and hue play in mate recognition and sexual selection, only recent studies have begun to address the causative factors involved in their evolution. Seehausen and colleagues (2008) provide the most comprehensive and insightful examination female preference and male hue evolution to date. This work examines the sensory drive hypothesis along an environmental transect in Lake Victoria. In their exhaustive study, the authors demonstrate correlated changes in male color pattern, frequencies of opsin alleles with differing sensitivities, female mate preference for male hue, and ambient light along an environmental gradient. This study examined the crucial links between female preferences, visual physiology, and the environment and in doing so provides one of the most comprehensive explanations of male color pattern and female mate choice diversity in cichlid fishes.

Females are not the only sex to exhibit mating preferences based on color patterns. Males also exhibit mating preferences for sex-linked female color patterns. This preference appears to be inherited and may contribute to formation of new species (Pierotti et al. 2008). However, male mating preferences vary considerably within populations indicating high dynamics of this trait (Pierotti et al. 2008). Additionally, natural selection may limit the divergence of coloration due to its role in camouflage and adaptation to habitat (Salzburger 2009).

Sand Bowers

Males of sand dwelling cichlids often build sand bowers which are used to attract females. These bowers represent extended male visual phenotypes which are of species-specific size and shape (McKaye et al. 1990; McKaye et al. 1993; Rossiter and Yamagishi 1997; Stauffer et al. 2002; Kidd et al. 2006). These bowers are solely used as display sites to attract females (McKaye et al. 1990; Tweedle et al. 1998) which prefer conspecific bower shapes. Hence, this character has the potential to cause reproductive isolation among closely related sand-dwellers (McKaye et al. 1993). Often bowers of numerous males are organized in leks, where males display to passing females (Tweedle et al. 1998). Females move over the lek and mate with several males (McKaye 1991; Stauffer et al. 2002).

Studies suggest that female mate choice shapes the bower architecture. For example, in a number of species, males with taller bowers have higher breeding success (McKaye et al. 1990; Stauffer et al. 2005). Young et al. (2009) tested for a model explaining lek formation and found support for the “female preference” model. This model predicts that females prefer mating with males which are aggregated in clusters, because of a reduction of predation risk, easier male comparison (more males, shorter distances), and higher quality of lek forming males. Males experience a higher per capita female encounter rate with increasing lek size. Hence, both sexes benefit from lek formation. Yet, nothing is known about the genetic basis and heritability of bower formation and preference (Kidd et al. 2006).

18.3.3.2 Non-visual Cues

Recent evidence suggests that visual communication is insufficient to explain the diversity of East African cichlids and the maintenance of species boundaries among closely related species (Plenderleith et al. 2005; Blais et al. 2009). Consequently, additional cues such as olfaction and acoustic signaling have been suggested to play an important role in mate choice (Robinson et al. 1998; Knight and Turner 1999; Amorim et al. 2003; Amorim et al. 2004; Plenderleith et al. 2005; Cole and Stacey 2006; Blais et al. 2009).

Acoustic Communication

Studies of cichlid sound production have shown that cichlids employ acoustic communication in a variety of social interactions (Lobel 1998; Nelissen 1978; Ripley and Lobel 2004; Amorim et al. 2003, 2004, 2008; Simões et al. 2006, 2008; Danley et al., unpublished). Acoustic signals may be used for the identification of conspecific mates and the evaluation of male quality (Simões et al. 2008). Acoustic signals are also employed by males (Amorim et al. 2003; Amorim and Almada 2005; Simões et al. 2008; Longrie et al. 2008) and females (Simões et al. 2008) during antagonistic interactions. These observations are in accordance with the use of acoustic signals in a wide array of other fish taxa (Lobel 1992; Kihslinger and Klimley 2002; Amorim 2006 for reviews). A recent study identified differences in various acoustic parameters among closely related species of rock-dwelling cichlids and even geographic differences within species suggesting the presence of local acoustic dialects (Danley et al., unpublished). Variation in acoustic signals has already been demonstrated in the whitetail shiner, *Cyprinella galactura* (Phillips and Johnston 2008). However, future studies need to evaluate the within and between population divergence of sound parameters and the importance of this variability in the mate recognition systems of these species.

Chemical Communication

Chemical communication in cichlid fish is a little explored area. However, previous studies suggest that olfaction is used in a variety of social contexts; females may employ olfactory cues to identify conspecific males (Plenderleith et al. 2005), and olfaction maybe used for the recognition of conspecifics in general (Giaquinto and Volpato 1997). Furthermore, olfactory cues emitted with urine appear to be important social signals and can indicate social status (Almeida et al. 2005; Barata et al. 2007, 2008). The use of electro-olfactograms (EOG) indicates that steroid hormones or steroid-like compounds may be the functional components in urine (Cole and Stacey 2006; Frade et al. 2002; Barata et al. 2008). The importance of chemical cues in cichlid communication is not universally supported; work by Jordan et al. (2003) and Venesky et al. (2005) rejected olfaction as important mate choice cue for Lake Malawi rock-dwellers.

18.3.3.3 Multimodality of Premating Cues

This review of cichlid communication and mate choice suggests that single traits alone are not sufficient to explain the species diversity and maintenance of reproductive isolation (Plenderleith et al. 2005; Blais et al. 2009). More likely, various communication modalities may act in different situations during mating or over different distances. Smith and van Staaden (2009), for example, showed that visual and acoustic communication modalities are associated; the same is probably true for olfaction, and combinations of all cues, but this remains to be tested.

It has been suggested that species richness is a function of the number of traits involved in diversification (Nosil and Harmon 2009). Likewise, Galis and Metz (1998) stated that “a large number of independent elements increases the number of potential solutions for a particular. . .problem.” They used this argument as hypothesis for the tremendous diversity of jaw morphologies, but the same may apply for mating systems. Hence, involvement of multiple communication systems, such as vision, olfaction, and acoustics, would allow for a greater number of taxa. Each of those traits can comprise multiple modalities itself. Visual traits, for example, can be subdivided into shape, pattern, and hue, whereas different acoustic parameters, including frequency, trill period and pulse period could serve different functions for mate recognition. Furthermore, species may vary in the relative importance of different modalities. For example, cichlids living at great depths in relatively poor photic environments may rely on acoustic and olfactory cues to a greater degree than species living in shallow in-shore areas of the lakes. The multimodal nature of mate recognition and evaluation within cichlids provides a greater phenotypic space for mating signals to diversify, potentially contributing to the high observed diversity of cichlid fishes.

18.3.4 Genetic Factors Influencing Speed and Richness of Divergence

18.3.4.1 Retention of Ancestral Polymorphisms

The large amount of shared genetic variation found within the East African species flocks has both fascinated and stymied evolutionary biologists. While Lake Tanganyika species tend to be reciprocally monophyletic using mtDNA (Sturmbauer and Meyer 1992; Sturmbauer et al. 2003), the younger Lake Victoria and Malawi cichlids share mtDNA haplotypes among species (Meyer et al. 1990; Moran and Kornfield 1993). Limited success has been achieved in resolving some clades in these systems using a nuclear genomic multilocus marker system (AFLP) (Albertson et al. 1999; Koblmüller et al. 2007b; Koblmüller et al. 2008b); still, the majority of relationships within the haplochromine cichlids remain unresolved. The use of single nucleotide polymorphisms (SNP) may provide additional resolution. However, a study performed by Loh et al. (2008) suggests that shared polymorphism at SNP loci is also common. Historically, the high level of shared genetic diversity has been attributed to the very recent age of the Lake Malawi diversification, the lack of fixation of neutral markers, and, consequently, the retention of ancestral polymorphism (Moran and Kornfield 1993). More recent studies have focused on the role that hybridization may play in preventing the fixation of alleles within a lineage.

18.3.4.2 Hybridization

Hybridization has long been thought to slow down evolutionary change (Seehausen et al. 1997). More recent evidence suggests that hybridization could contribute to the evolution of phenotypic novelty, increase genetic diversity within species (Rüber et al. 2001; Salzburger et al. 2002a; Seehausen 2004) and possibly contribute to the creation of new species by introducing new genetic variation in the hybrid population (Albertson and Kocher 2006; Koblmüller et al. 2007b). It was also argued that hybridization may produce more fit individuals via transgressive segregation, especially if newly formed species possess alternative alleles that are not yet fixed (Seehausen 2004; Bell and Travis 2005; Rieseberg 1999). Traits under strong directional selection, however, are likely to be fixed for alternative alleles. Strong directional selection may limit the degree to which novel phenotypes are produced by hybridization (Albertson and Kocher 2005). However, Parnell et al. (2008) argue that the phenotypic limitations imposed by genetic architecture can be overcome in hybrids even in the presence of strong directional selection. These authors argue against measuring individual morphological elements and for viewing the phenotype as a functional unit that can be arrived at through multiple mechanisms. As an example, they discuss various ways in which the components of the jaw can be structured to produce similar kinematic transmission of the oral jaws. The importance of hybridization in generating genetic and phenotypic novelty is becoming more widely recognized in cichlids and other systems.

18.3.4.3 Gene/Genome Duplication

Gene duplication, whether at the gene or genome scale, makes one of the copied regions redundant and therefore reduces the strength of selection on one of the duplicates. One or both of the copies, therefore, can evolve to take on a more specialized function (subfunctionalization) or may even acquire a new function (neofunctionalization). As a result, gene (or genome) duplication may lead to phenotypic divergence (Ohno 1970). Some authors have suggested that the diverse color patterns seen in East African cichlids, which have been implicated in their extraordinary divergence, may be the result of gene duplications. Within cichlids Watanabe et al. (2007) identified a gene duplication event of *kir7.1*, an inwards rectifier potassium channel that is known to influence zebrafish color pattern. However, the function of *kir7.1* in cichlids remains unknown since the cichlid paralogs (*cikir7.1* and *cikir7.2*) do not appear to be expressed in zebrafish (Watanabe et al. 2007). The duplication of *kir7.1* is only one of many genes involved in pigmentation that have been duplicated in bony fishes. As noted by Braasch et al. (2006), bony fish have duplicates of the pigmentation genes *mitf*, *sox10*, *tryrosinase*, *csf1r, pdgfrb*, and *kit* (Braasch et al. 2006 and references therein). Braasch et al. (2006) suggest that the fish-specific genome duplication (FSGD) event led to the duplication and neofunctionalization of two physically linked type III receptor tyrosine kinases (RTKs) known to influence vertebrate color patterns. One paralog appears to have retained its traditional function, while the other appears to have taken on a novel function. The authors conclude that genome duplications, including the FSGD event, contributed to increased number of pigment cell types in fishes (Braasch et al. 2006).

Possibly one of the best studied examples of gene duplication involvement in the evolution of phenotypic novelty, and species divergence has been discovered through studying the duplication of opsin genes. Five opsin gene types are found in many vertebrates. Opsin genes can be distinguished based on the wavelength of light to which they are most sensitive [Short wavelength Sensitive 1 (*SWS1*), Short wavelength Sensitive 2 (*SWS2*), Rhodopsin class (*Rh1*), Rhodopsin Like (*Rh2*), and Long wavelength Sensitive (*LWS*)] (Hoffmann and Carleton 2009 and references therein). The *SWS2* and the *RH2* genes both have been duplicated early in the divergence of teleosts. *RH2* experienced a secondary duplication within cichlids. Each of these duplication events appears to have been through tandem duplication. As a result, cichlids possess eight functional opsin genes (*SWS1*, *SWS2A*, *SWS2B*, *Rh1*, *Rh2Aa*, *Rh2Ab*, *Rh2B*, and *LWS*), though, generally, only three cone opsins and a rod opsin are expressed at any given time. The cichlid visual system can, therefore, be tuned through the selective gene expression of these opsin genes to match their spectral environment (Hoffmann and Carleton 2009). The system can be further tuned through the segregation of alleles at these loci for minor changes in wavelength sensitivity (Seehausen et al. 2008). The divergence of opsin genes and alleles is thought to have provided cichlids with the raw material necessary for divergence through sensory drive to occur (Seehausen et al. 2008). The role that gene duplication plays in species divergence is beginning to appear as a more general phenomenon not limited to cichlids (Horth 2007).

18.3.4.4 Linkage Disequilibrium

Theoretical and empirical work has examined the role that linkage, both genetic and physical, can play in the rapid phenotypic evolution and speciation (Hawthorne and Via 2001; Rundle and Nosil 2005; Dobzhansky 1951; Orr 2005; Kocher 2004). Linkage disequilibrium results from the nonrandom association of alleles at separate loci. As a result, selection on one allele results in the correlative selection of linked alleles at different loci. Selection acting on one phenotype can influence the evolutionary trajectory of a seemingly independent phenotype. This pattern is of particular interest to evolutionists when one of the loci is under strong natural selection and the other loci influence mating behavior and/or reproductive isolation.

Within cichlids, Albertson et al. (2003) found that quantitative trait loci (QTL) contributing to tooth and neurocranium shape in cichlids are linked not only to each other but also appear to be linked to genes contributing to sex determination. This has led some researchers to hypothesize the existence of “speciation chromosome” in Lake Malawi’s cichlids (Streelman and Albertson 2006). More recently, Roberts et al. (2009) identified a region within the *Pax7* gene that determines pigmentation patterns in many Lake Malawi cichlids. Individuals with one allele have a “wild-type” pigmentation pattern, while individuals with the alternative allele have a disrupted pigmentation pattern referred to as orange bloched or OB. The OB pattern is believed to confer a degree of crypsis (Roberts et al. 2009). However, the OB pattern, when expressed in males, disrupts nuptial coloration potentially causing a break down in the mate recognition system. Therefore, the OB allele is believed to be under sexually antagonistic selection: it is beneficial in females but costly in males. This conflict is believed to have been reduced by the invasion of a dominant female sex determining allele with tight linkage to the OB allele. Under such a system, individuals inheriting the OB allele would most often be female.

Roberts et al. (2009) suggest that in systems with strong sexual selection, such as East African cichlids, the costs of evolving novel phenotypes which confer opposing fitness values to the different sexes can be minimized through tight linkage to sex determining loci. In this way, novel phenotypes can evolve and spread even when in sexual conflict. Yet conflicting sex-determining systems may lead to genetic incompatibilities between nascent species and further strengthen reproductive isolation in these species.

18.4 Biological Conservation Issues

While terrestrial ecosystems are reasonably well protected, this is not the case for most African aquatic ecosystems. If applied, conservation strategies for aquatic biota have so far been the same as for terrestrial environments, i.e., by declaring biodiversity hotspots national parks. However, it seems questionable that this strategy will work, given the strong micro-geographic structure of the species flocks and the great degree of local endemism.

The current threats are not (yet) caused by habitat destruction and pollution but by overharvesting. Local fishermen and commercial companies developed a strong interest for exploiting the three great lakes. So far, commercial fisheries focused on large or abundant non-cichlid fishes such as the endemic Nile perches or sardines in Lake Tanganyika, the introduced Nile perch in Lake Victoria, and on endemic pelagic cichlids in Lake Malawi. Near-shore fish communities were only targeted by artisanal fishermen, which – due to their unprofessional equipment – could not harm them considerably (Coulter 1991). Commercial fishing activities face increasing problems due to overfishing, and governments reacted by enacting catch regulations. Yet, these are difficult to enforce in large lakes across national borders. In addition to the regulating efforts of governmental Fisheries Departments, stocks seemed somehow self-regulated, in that the high gasoline price made inefficient catches financially impossible for the large vessels. The reduced activities of the larger companies gave the stocks at least some time to recover. However, at least in Lake Tanganyika, the fishing strategy of the large commercial companies changed recently, towards supporting a franchise system by distributing outboard engines to local fishermen, which are to be paid for in fish returns (H. Phiri, Department of Fisheries Chilanga, personal communication). The effects of this boosted activity of local fishermen on the fish communities will be seen in the near future. The transport of frozen fish to distant markets was also decentralized, in that now not only the trucks of commercial companies deliver fish to larger cities, but also small cool-houses and trucks sustain several one-man companies. Given the enormous demand, pelagic fish communities are certainly at risk.

The second change in the fishing strategy of artisanal fishermen concerns littoral cichlid fishes. Instead of using gillnets alone and leaving them in the water for several hours, a new strategy can be observed in Lake Tanganyika: snorkeling masks and gill nets are increasingly used by local fishermen. They use the same strategy as commercial ornamental fish catchers and snorkeling fishermen can easily target large littoral fish species on rocky and muddy substrates. Instead of placing the net in the water to specifically catch fish of the size class fitting the mesh size, divers strategically place the gill nets to actively chase in all large individuals. Near villages large specimens almost disappeared (Toby Veall, personal communication).

A recent essay suggested a novel strategy for protecting African Lake communities that accounts for their patchy distribution and local endemism (Sturmbauer 2008). The concept is analogous to the source and sink metapopulation model (Hanski and Simberloff 1997) whereby some subpopulations are being steadily harvested (sinks) and others serve as stabilizing sources (Dias 1996; Weiss 2005). The suggested strategy was derived from recent molecular phylogenetic and phylogeographic studies on East African cichlid fishes and fisheries data. It noted the following peculiarities of the endemic communities in the East African Great Lakes: While connectivity is the major problem for species in terrestrial and marine national parks (Soule 1980; Franklin 1980; Ryder 1986; Moritz 1994), to ensure a large enough effective population size of the protected animals, this is not the case in most taxa of African rivers and lakes, where microgeographic endemism prevails. Unlike many other organisms, cichlid fishes are poor dispersers. For example, most littoral cichlid species are subdivided into numerous distinct "color morphs" with restricted distribution (Sturmbauer and Meyer 1992; Verheyen et al. 1996; Rüber et al. 1999); small offspring numbers further contribute to the problem.

Sturmbauer (2008) argued that the establishment of "microscale protected areas," a large number of small stretches of strictly protected coast line, each only some hundreds of meters long, is likely to work best to preserve the littoral cichlid communities in African lakes. Such protected zones can sustain a reasonably effective population size of littoral species, serve as spawning ground or nursery areas for pelagic species, and at the same time reseed all neighboring populations that are exploited continuously. A similar conservation strategy was recently suggested for Indo-Pacific grouper species, and the establishment of small "no-take-areas" increased the population of most grouper species by 30% over 5 years of protected status (Unsworth et al. 2007). The study on groupers also showed that a stretch of 500 m of protected area was enough to increase the population of top predatory fish. As long-term stability of littoral fishing grounds is in the immediate interest of village communities, such small protected areas should be managed and controlled by the local communities themselves, while supervised by governmental institutions.

Species diversity is not only threatened by anthropogenic causes but also by evolutionary factors. Gavrilets and Losos (2009) propose that species numbers in Lakes Victoria and Malawi will generally decline and become more similar to those observed in Tangyanika through evolutionary mechanisms. Repeated cycling of allopatric divergence and secondary admixis of the diverged species, termed species pump by Rossiter (1995), will have the following effects on species communities: Secondary admixis events will place ecologically equivalent sister species in sympatry and direct competition. Such competitive interactions might often drive one competitor to extinction, while the distribution ranges of successful species will progressively increase (Sturmbauer 1998). In this way, species communities will be slowly homogenized along larger shore sections, and overall species numbers are likely to decrease. This scenario would explain the relatively small estimated total number of 250 endemic cichlid species in Lake Tanganyika, compared with the 500+ species of the much younger Lake Victoria and the 500–700 species of Lake Malawi with its intermediate age.

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Chapter 19
Inter- and Intraspecific Genetic Biodiversity in South East Asian Rodents: New Insights for Their Conservation

Marie Pagès, Alice Latinne, and Michaux Johan

Abstract South East Asia displays a high level of mammal endemism and the highest number of threatened and data deficient mammal species. However, the South East Asian biodiversity is still highly unexplored. Because of the runaway global changes, a better biological knowledge of this region is urgently required to improve the conservation and the management of its biodiversity.

The first aim of this chapter is to present recent published data on a biodiversity inventory of the Rattini murine rodents from this region based on molecular markers (Pagès et al., 2009). In this first study, we applied the method proposed by Pons et al. (2006) that determines with no a priori the locations of ancestral nodes that define putative species in order to investigate the current taxonomy of the Rattini tribe.

Our second aim concerns the intraspecific genetic structure of a rare and threatened South East Asian mammal species: the murine rodent *Leopoldamys neilli*, endemic to karst habitats . In this latter study, our results evidenced a high geographic structure of the genetic diversity of this species. The observed highly divergent genetic lineages would have to be considered as distinct evolutionary units or at least as Management units. These results are essential for the best conservation issues of species endemic to karsts and to South East Asia, in general.

In this chapter, we therefore highlight that South East Asia would not be only a hotspot of interspecific but also of intraspecific biodiversity.

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19.1 Introduction

South East Asia overlaps with four hotspots of biodiversity containing exceptional concentrations of endemic species and facing huge habitat loss (Myers et al. 2000). Relative rate of deforestation is higher in South East Asia than in any other tropical regions (Achard et al. 2002) and threatened species of the world's land mammals are mainly concentrated in this area (Schipper et al. 2008). However, the biodiversity of South East Asia is still highly unexplored, even for large vertebrates (e.g., mammals) and new mammal species are yearly described (e.g., *Laonastes aenigmamus*, Jenkins et al. 2005; *Saxatilomys paulinae*, Musser et al. 2005; *Mayermys germani*, Helgen 2005; *Tonkinomys daovantieni*, Musser et al. 2006). An increase of biological knowledge of this region is therefore urgently needed to improve the conservation of South East Asian biodiversity (Sodhi et al. 2004).

The first aim of our researches in this region was to develop a biodiversity inventory and a taxonomic review of the Rattini Murine rodents from South East Asia based on molecular markers. Indeed, among Muridae rodents, the Rattini tribe includes 35 genera corresponding to 167 rat species (Musser and Carleton 2005). Almost all representatives of this tribe inhabit South East Asia, a region confronted to an ongoing economic growth damaging habitats and biodiversity (Matosi 2005; Forman et al. 2008). While the division of the tribe into five groups (i.e. *Crunomys*, *Dacnomys*, *Maxomys*, *Micromys,* and *Rattus* divisions) (Musser and Carleton 2005; Lecompte et al. 2008) is widely accepted, its taxonomy remained, however, largely unexplored phylogenetically and its delimitations were not yet defined. Although easily recognized at a generic level by an expert, Asian rats are often difficult to identify at a specific level using morphological or cytological criteria. The wide range of intra-specific morphological variation makes morphological criteria unsuitable for accurate rat species identification and has led to a confusing taxonomy. DNA-based methods, however, appear to be promising tools for straightforward and reliable rat species-specific identifications (Badenhorst et al. 2009). In this first published study, we sequenced two mitochondrial and one nuclear genes from rat specimens coming from South East Asia (Thailand, Cambodia and Lao People's Democratic Republic) to perform phylogenetic reconstructions. Then, as morphological characters are often confusing, we applied the method developed by Pons et al. (2006) that determines, with no a priori expectations, the locations of ancestral nodes to define putative species. This part of the paper will summarize the results obtained by our team and which are more largely developed in Pagès et al. (2010).

The second aim of our researches was to detect the biodiversity at a finer scale than the species level (intraspecific biodiversity) using phylogeographic approaches. Indeed, in contrast to other regions in the world, the South East Asian region is poorly studied on this point of view, as only 3.3% of the phylogeographic studies published between 1987 and 2006 concern taxa from this region (Beheregaray 2008). However, our taxonomic and phylogenetic studies evidenced the existence of important intraspecific genetic variability within several of the studied Rattini species. Phylogeographic approaches, therefore, appear highly important to better understand the level of South East Asian biodiversity, not only on the interspecific but also intraspecific level.

Moreover, some specific habitat types remain particularly unexplored in South East Asia despite their high putative scientific interest and biological importance (Sodhi et al. 2004). Limestone karsts of South East Asia are one of these ignored habitats needing further investigations (Clements et al. 2006). Limestone karsts are sedimentary rock outcrops consisting of calcium carbonate created millions of years ago by calcium-secreting marine organisms, and subsequently lifted above sea level by tectonic movement (Clements et al. 2006). Karsts are widespread throughout South East Asia where they cover an area of 460,000 km^2 (Day and Urich 2000). Due to the high level of endemic species of plants, vertebrates and invertebrates they support (Vermeulen and Whitten 1999: Schilthuizen et al. 2005; Clements et al. 2006, 2008) and the high threats they are facing such as unsustainable limestone quarrying, deforestation, hunting, and urbanization (Vermeulen and Whitten 1999; Clements 2006), karsts are thought to be a hotspot of biodiversity of high biological importance.

For these reasons, we focused on the phylogeographic structure of one threatened murine rodent species, endemic to limestone karsts of Thailand, *Leopoldamys neilli*. This species is a large and long-tailed rat with a grayish-brown fur and white belly. It was discovered in 1973 in the Saraburi province, Thailand (Marshall 1977). The species has been recorded in few locations in northern and south western part of peninsular Thailand (Lekagul and McNeely 1988; Waengsothorn et al. 2007). Very little information is available about its biology and its ecology. *L. neilli* was previously classified as an endangered species on the IUCN Red List but is now listed as data deficient due to the lack of data available for this species (Lunde and Aplin 2008). Acquisition of data about its geographic range, genetic structure and ecological requirements is, therefore, critical to assessing its real conservation status.

19.2 Methods

19.2.1 Sampling

19.2.1.1 Taxonomic Review

Hundred and sixteen specimens of Rattini were selected among the 3,000 trapped by our team in the fields mostly in Thailand and punctually in Cambodia and in the Lao PDR. Specimens selected were chosen in order to maximize the number of species and geographic locations analyzed. Field identifications were made based on morphological criteria according to Wilson and Reeder (2005), Marshall (1977) and Aplin et al. (2003a). Field specimen identifications and locality information are detailed in Pagès et al. (2010).

19.2.1.2 Phylogeography of *L. neilli*

A total of 115 *L. neilli* collected (live-trapped) by our team in limestone karsts from 20 localities in seven provinces of Thailand (Loei, Nan, Phrae, Saraburi, Nakhon Ratchasima, Lopburi, Kanchanaburi provinces) has been analyzed. Field specimen identifications and locality information are given in Latinne et al. (2011).

All the collected animals were released after sampling a small piece of ear skin. The skin samples were stored in ethanol. Two specimens of *Leopoldamys edwardsi* collected by our team were chosen as outgroup.

19.2.2 Sequence Acquisition

19.2.2.1 Taxonomic Review

Three genes proven valuable for rodent systematics were considered for the phylogenetic analyses (Jansa and Weksler 2004; Jansa et al. 2006; Robins et al. 2007; Lecompte et al. 2008): two mitochondrial markers, the cytochrome *b* (cytb) and the cytochrome c oxydase I (COI) genes and the first exon of the nuclear gene encoding the interphotoreceptor retinoid binding protein (IRBP). DNA extraction and amplification are detailed in Pagès et al. (2010).

19.2.2.2 Phylogeography of *L. neilli*

Two mitochondrial markers, the cytochrome *b* gene (cytb) and the cytochrome c oxydase subunit I gene (COI), were amplified for all the samples. Moreover, a nuclear locus, the β-fibrinogen intron 7 (bfibr) (745 bp), was targeted for a subset of 65 samples representative of the main mitochondrial clades found, using primers designed by Seddon et al. (2001). DNA extraction and amplification are detailed in Latinne et al. (2011).

19.2.3 Phylogenetic Analyses

Sequences were aligned by eye using SEAVIEW (Galtier et al. 1996) or automatically aligned using BIOEDIT 7.0.9.0 (Hall 1999) and the ClustalW algorithm. Phylogenetic trees were reconstructed for the taxonomic and phylogeographic purposes using two probabilistic approaches: the maximum likelihood method (ML) and Bayesian inferences (BI) as described in Pagès et al. (2010) and Latinne et al. (2011).

A minimum spanning network was performed with ARLEQUIN 3.11 v4.5.1.6. (Bandelt et al. 1999) to explore relationships between haplotypes of the combined mitochondrial dataset (cytb/COI).

19.2.4 Species Delimitation Developed for the Taxonomic Review of the Rattini Tribe: DNA-Based Species Delimitation Method

The DNA-based approach developped by Pons et al. (2006) was used as reported in Pagès et al. (2010). Using a likelihood framework, this method detects the shift in the rate of lineage branching of an ultrametric tree from interspecific long branches to intraspecific short budding branching and identifies clusters of specimens corresponding to putative species.

19.2.5 Species Identification

Sequences available in databanks were used to give a species name to each cluster identified as a putative species by the method of Pons et al. (2006). To do so, *Rattus* cytb (663 bp) and COI (655 bp) sequences obtained by Robins et al. (2007) were extracted from GenBank and added to our mitochondrial (*mt*) dataset. Two other unpublished cytb sequences of *R. argentiventer* and *R. sikkimensis* (synonym of *R. andamanensis*) provided by O. Verneau and F. Catzeflis were also included in the subsequent analysis. Sequences of a single representative of *Berylmys*, *Niviventer*, *Leopoldamys*, *Maxomys,* and *Micromys* were used to root our mitochondrial phylogeny. Therefore, the *mt* dataset included 129 sequences corresponding to 1,318 bp of *mt* DNA.

19.2.6 Genetic Diversity, Demographic History, and Divergence Times Among the Intraspecific Lineages of **L. neilli**

Haplotype (h) and nucleotide (π) diversities of the main lineages corresponding to the studied karstic regions were estimated for each locus using Arlequin 3.11 (Excoffier et al. 2005). An Analysis of Molecular Variance (AMOVA) performed on the two combined datasets (cytb/COI - cytb/COI/bfibr) in Arlequin 3.11 was used to assess the distribution of genetic variation among populations. The genetic groups were defined as detailed in Latinne et al. (2011).

To evaluate the demographic histories of the main lineages of *L. neilli*, the mismatch distribution of pairwise nucleotide differences was estimated in DNASP version 5 (Librado and Rozas 2009). Fu's Fs (calculated in Arlequin 3.11), Fu and

Li's F* & D* statistics (calculated in DNASP), and R2 (Ramos-Onsins and Rozas 2002) (calculated in DNASP) were also used to test for population growth under assumptions of neutrality. These demographic analyses were calculated only for populations including more than 15 samples for the cytb dataset.

Divergence times of *L. neilli* and *L. edwardsi* and of the main lineages of *L. neilli* (approximation of the time to the most recent common ancestor : TMRCA) were estimated under a relaxed molecular clock assumption using Bayesian inference (Drummond et al. 2006), as implemented in the program BEAST V1.5.3. (Drummond and Rambaut 2007). Sequences of *Mus musculus*, *Mus spretus*, *Rattus rattus,* and *Rattus tanezumi* were added to the dataset in order to use the *Mus/Rattus* divergence (10–12 million years ago) as a calibration point. An evolutionary rate of 2.6% generally observed for rodents (e.g., Michaux et al. 2003) was also used to estimate the TMRCA. Analyses were performed under the TN93+G substitution model parameter (previously estimated by MODELTEST), a relaxed molecular clock, and a Bayesian Skyline plot demographic model (Drummond et al. 2005). Three independent runs with MCMC chain length of 6.5×10^7 were performed, sampling every 1000th generation. Results were visualized using TRACER v1.5.

19.3 Results

19.3.1 Taxonomy of the Rattini Tribe

19.3.1.1 Sequence Analyses and Phylogenetic Reconstructions

BI, and ML analyses yielded the same topology given in Fig. 19.1. Most relationships among the Rattini tribe were well elucidated [supports 61–100 for Bootstrap (Bp), 0.82–1.00 for posterior probabilities (pp)]. Monophyletic groups corresponding to the Rattini divisions proposed by Musser and Carleton (2005) are supported with the highest values of Bp or pp. The *Maxomys* division undoubtedly appears as the earliest division to diverge followed by the *Dacnomys* division, here represented by *Leopoldamys* and *Niviventer* genera, and the *Rattus* division. *Berylmys* appears with the highest support values as the first lineage to diverge among the *Rattus* division. A sister grouping is obtained between the genera *Bandicota* and *Rattus*, but this association is weakly sustained. In fact, the monophyly of the *Rattus* genus received moderate pp (0.82) to weak Bp supports (61 for unpartitioned, 63 for partitioned ML analyses). Inside the *Rattus sp.* clade, the 3 *Rattus* species groups proposed by Musser and Carleton (2005) could be found. The *R. exulans* monotypic group (*Re*, Fig. 19.1) grouped with the *R. rattus* species group (*Rr*, Fig. 19.1) with high branch supports (Bp = 94/96 for the unpartitioned/partitioned ML analyses; pp = 1) and the *R. norvegicus* species group (*Rn*, Fig. 19.1) is placed as sister taxa to the *R. exulans* species group/*R. rattus* species group cluster.

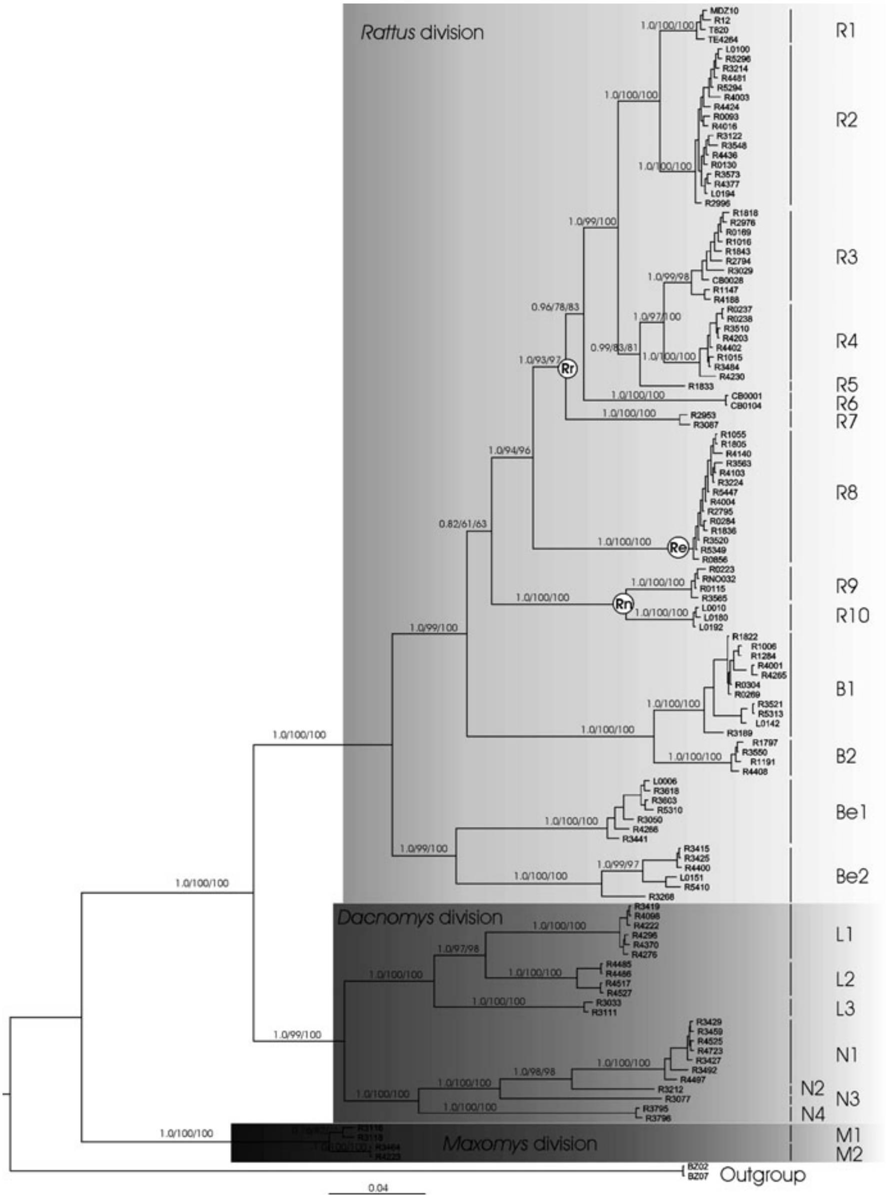

Fig. 19.1 Phylogenetic tree depicting relationships of the Indochinese Rattini based on the analyses of the combined cytb, COI and IRBP genes and reconstructed following Bayesian method. BI and ML analyses of the dataset gave an identical topology. Numbers above the branches reflect support obtained from the analysis of the dataset following 3 different reconstruction methods: BI/unpartitioned ML/partitioned ML. Support values (Bp and Pp) are not shown for very short branches. The symbol "**" indicates that phylogenetic relationships are not supported by the partitioned ML analysis. **Rr** stands for *Rattus rattus* species group, **Re** for *Rattus exulans* species group, **Rn** for *Rattus norvegicus* species group, following Musser and Carleton's (2005)

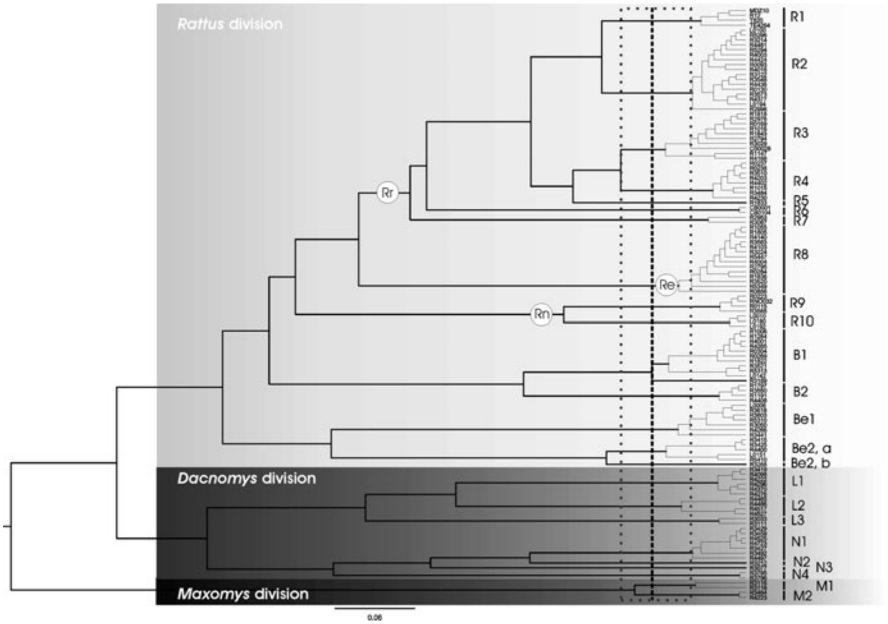

Fig. 19.2 Rattini ultrametric tree based on the combined mitochondrial and nuclear datasets obtained with Multidivtime and clusters of specimens recognized as different species by the method of Pons et al. (2006). Genetic clusters recognized as a valid species are highlighted in red and separated by longer black branch. The vertical bars group all sequences within each significant cluster, labeled R1 to M2 according to the genus to which they belong. **Rr** for *Rattus rattus* species group, **Re** for *Rattus exulans* species group, **Rn** for *Rattus norvegicus* species group (modified from Pagès et al. 2010)

At this point in the analysis, 23 lineages (labeled R1 to M2 in Fig. 19.2) were identified within our taxon sampling. As their specific status is still questionable, intra-generic relationships are problematic to describe and cannot be discussed at present.

19.3.1.2 Species Delimitation

The existence of distinct phylogenetic lineages was corroborated by the analysis of the branching rate pattern. The analysis led to an estimate of 24 putative species, 4 of which encompassing a single individual (labeled R5, Be2b, N2, and N3, respectively, in Fig. 19.2). Two *Maxomys* (M1 and M2), 4 *Niviventer* (N1 to N4),

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Fig. 19.1 (continued) denominations. At the right hand of the tree, lineages are labeled according to the genus to which they belong (Genera *Rattus*, *Berylmys*, *Leopoldamys*, *Niviventer*, *Maxomys*) (modified from Pagès et al. 2010)

3 *Leopoldamys* (L1 to L3), 2 *Bandicota* (B1 and B2), 3 *Berylmys* (Be1, Be2a, Be2b), and 10 *Rattus* species (R1 to R10) could be numbered as provided in Fig. 19.2. It is worth noting that the *Berylmys* lineage (labeled Be2) actually seems to correspond to two putative species following Pons et al's approach (therefore, labeled Be2a and Be2b in Fig. 19.2).

19.3.1.3 Species Identification

The partitioned ML analysis of the *mt* dataset including 64 *Rattus* sequences (Pagès et al. 2010) plus 61 from previous studies (Robins et al. 2007) gave the highly resolved and robust tree given in Fig. 19.2. This has allowed us to name some clusters identified as putative species by the DNA-based species delimitation method. Because the monophyly of each cluster embracing the supplementary published sequences is supported with the highest Bp value, the level of confidence of these identifications could be considered as maximal if the voucher identification beforehand is correct.

Robins' sequences identified as *Rattus rattus* group with 100% Bp support with sequences identified as *R. rattus* specimens in Tollenaere et al. (2010). Specific identification of group R1 as *Rattus rattus* is thus compellingly confirmed. According to the *mt* tree, none of the samples from Thailand, Cambodia, or the Lao PDR could be assigned to this species. Following the same approach, R2 seems to correspond to *Rattus tanezumi*, R5 to *Rattus tiomanicus*, R8 to *Rattus exulans,* and R9 to *Rattus norvegicus*. Sequences provided by *O. Verneau* and *F. Catzeflis* allowed us to identify R6 as *R. argentiventer* and R7 as *R. andamanensis*. The situation appears more problematic for the species R3. This group corresponds to a mix of specimens identified as *R. rattus diardi* in Robins et al. (2007), *Rattus kandianus* (considered as a synonym of *R. rattus* in Musser and Carleton 2005), *R. tanezumi* from Indonesia (Robins et al. 2007) and *R. tanezumi*, *R. andamanensis,* or *R. argentiventer* according to the field names we assigned during our sampling. Consequently, no nominal species could be reliably assigned to R3. According to morphological criteria and because of its sistership with *Rattus norvegicus*, R10 could be convincingly assigned to *Rattus nitidus*.

19.3.2 Phylogeography of L. neilli

19.3.2.1 Phylogenetic and Phylogeographic Analysis

The two mitochondrial genes yielded weakly supported phylogenies and gave generally the same topologies. Therefore they were combined into one matrix, yielding a better resolved phylogeny. The minimum spanning network for this

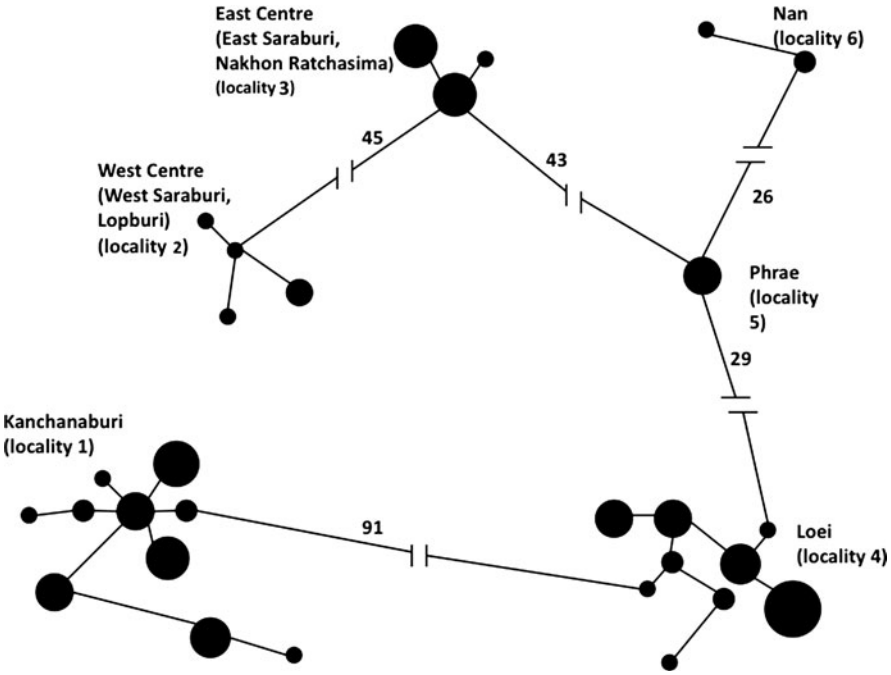

Fig. 19.3 Minimum Spanning network constructed using the 29 haplotypes of mitochondrial dataset. Geographic origins (Table 19.1) are noted. Numbers correspond to the mutational steps observed between haplotypes. The size of the circles is proportional to the numbers of individuals corresponding to each haplotypes. The localities were the haplogroups were observed are also indicated (see Fig. 19.4) (modified from Latinne et al. 2011)

mitochondrial DNA dataset (29 haplotypes) generated six main haplogroups corresponding to the six main study areas (Loei, Nan, Phrae, Saraburi-Nakhon Ratchasima, Lopburi, Kanchanaburi provinces). These groups are clearly isolated and separated by a very high number (26–91) of mutational steps (Fig. 19.3). The ML and Bayesian analyses yielded the same patterns, the monophyly of the haplogroups being very well supported (Bp: 100% – pp: 1.0) (see Latinne et al. 2011).

In order to associate phylogenetic information of the mitochondrial and nuclear markers and as the three genes yielded compatible topologies, we combined them in one dataset.

The network, ML, and Bayesian analyses of the three combined genes gave the same topology as with the two mitochondrial genes. Haplotypes clustered in six geographically well-structured haplogroups separated by a high number of mutational steps (from 31 to 99) and well resolved (Bp: 100% – pp: 1.0) (data not shown).

It is important to note that all these analyses evidenced an important genetic differentiation of the animals from Kanchanaburi (e.g., at least 91 mutational steps separating them) as compared to all the other populations.

19.3.2.2 Genetic Diversity and Population Differentiation

Haplotype and nucleotide diversities were calculated for the six main lineages for the three markers (cytb, COI, bfibr) taken separately. The results are presented in Table 19.1 and indicate that each lineage was characterized by a very low level of genetic diversity for all the markers. The genetic divergence (% K2P distance) within each lineage was also very low (between 0 and 0.04% for all markers).

The AMOVA performed on the mitochondrial dataset showed that 95.81% (93.74% for the three combined genes dataset) of variation is explained by differences among geographical lineages whereas only 2.20% (2.13%) and 2.00% (4.13%) of this variation are explained by differences among populations within lineages and within populations, respectively. These results are confirmed by the high genetic divergence (% K2P distance) (calculated only on the cytb dataset to allow comparison with other studies) observed between the lineages (Table 19.2).

19.3.2.3 Demographic History

Fu and Li's F* and D* as well as the R2 indices were not significant for all lineages. Fu's Fs values were not significant and evidenced values around 0 or slightly positive (see Latinne et al. 2011 for further details). All these results suggest a signal of stable populations or populations in low regression.

Table 19.1 Genetic diversity observed within the main genetic lineages of *Leopoldamys neilli* for the three loci

Locus	Lineages	Locality codes (see Fig. 19. 4)	Sample size	Number of haplotypes	Haplotype diversity (h ± SD)	Nucleotide diversity (π ± SD)	Genetic divergence within each lineage (K2P distances)
cytb	Kanchanaburi	1	43	7	0.81 ± 0.03	0.0032 ± 0.002	0.003
	Center West	2	6	3	0.60 ± 0.21	0.0011 ± 0.001	0.001
	Center East	3	17	3	0.59 ± 0.06	0.0013 ± 0.001	0.000
	Loei	4	40	6	0.79 ± 0.04	0.0024 ± 0.001	0.001
	Phrae	5	6	1	0.00 ± 0.00	0.0000 ± 0.000	0.000
	Nan	6	3	2	0.67 ± 0.31	0.0022 ± 0.002	0.003
COI	Kanchanaburi	1	43	5	0.61 ± 0.08	0.0019 ± 0.0013	0.002
	Center West	2	6	3	0.73 ± 0.15	0.0021 ± 0.0017	0.002
	Center East	3	17	1	0.00 ± 0.00	0.0000 ± 0.0000	0.000
	Loei	4	40	4	0.19 ± 0.08	0.0007 ± 0.0007	0.001
	Phrae	5	6	1	0.00 ± 0.00	0.0000 ± 0.0000	0.000
	Nan	6	3	2	0.67 ± 0.31	0.0009 ± 0.0012	0.001
bfibr	Kanchanaburi	1	28	5	0.64 ± 0.09	0.0057 ± 0.0033	0.002
	Center West	2	6	2	0.33 ± 0.21	0.0002 ± 0.0000	0.000
	Center East	3	11	1	0.00 ± 0.00	0.0000 ± 0.0000	0.000
	Loei	4	12	4	0.68 ± 0.10	0.0054 ± 0.0032	0.004
	Phrae	5	5	3	0.70 ± 0.22	0.0058 ± 0.0040	0.003
	Nan	6	3	1	0.00 ± 0.00	0.0000 ± 0.0000	0.000

Table 19.2 Genetic divergence between lineages [% K2P distance (lower diagonal) and net distance taking into account ancestral polymorphism (upper diagonal)] for the cytb dataset

	Loei	Nan	Phrae	Center East	Center West	Kanchanaburi
Loei		0.023	0.015	0.031	0.032	0.065
Nan	0.025		0.015	0.033	0.038	0.057
Phrae	0.015	0.017		0.023	0.028	0.061
Center East	0.031	0.034	0.023		0.027	0.065
Center West	0.033	0.040	0.029	0.027		0.071
Kanchanaburi	0.067	0.059	0.062	0.067	0.073	

The mismatch distribution for the mitochondrial dataset evidenced a multimodal pattern for all the lineages suggesting a stable population signal for each of them (see Latinne et al. 2011). The same pattern was observed when the three combined genes were analyzed.

19.3.2.4 Divergence Time Analyses

The estimations of the TMRCA using either the *Mus*/*Rattus* separation as fossil calibration point or the general evolutionary rate for rodents estimated at 2.6% per million year, gave the same results:

- A separation of *L. neilli* to the other *Leopoldamys* species at the end of the Tertiary, around 2.75–3.5 million years ago.
- The separation of the *L. neilli* population from Kanchanaburi to the other populations of Thailand around 1.8–2 million years ago.
- The differentiation of the remaining populations of *L. neilli* (Saraburi, Loei, Phrae, Nan regions), around 0.9–1.4 million years ago.

19.4 Discussion

19.4.1 Phylogenetic Relationships Within the Rattini Tribe

Our phylogenetic analyses of Indochinese Rattini based on the combination of cytb, COI, and the first exon of the IRBP genes are consistent with the revised taxonomy of Rattini divisions performed by Musser and Carleton (2005). The *Maxomys* division, the *Dacnomys* division (here consisting of *Leopoldamys* and *Niviventer* as sister taxa), and the *Rattus* division (here including the genera *Rattus*, *Bandicota,* and *Berylmys*) are supported with the highest support values (Fig. 19.2). These results are congruent with the murine phylogeny obtained by Lecompte et al. (2008) based on the analysis of the combined cytb, IRBP and GHR genes. In this latter analysis, the three divisions are well supported, and the *Maxomys* division is also the first to diverge followed by the *Dacnomys* one and the *Rattus* group sensu stricto of Verneau et al. (1997).

19.4.2 Toward a Deep Taxonomic Revision of the Rattini Tribe

At a specific level, phylogenetic relationships are difficult to disentangle. Species misidentifications were indeed plentiful and recurrent both in our sampling and in the literature. *Mt* sequences from Robins et al. (2007) provided by O. Verneau and F. Catzeflis were included in our dataset but questions about the reliability of the identification of vouchers were rapidly raised (see examples mentioned in Pagès et al. 2010). All in all, these reports (Robins et al. 2007; Verneau et al. 1997 and this study) stress the need of a sound taxonomic revision of the Rattini tribe. Consequently, one must first determine valid species boundaries and then assign an appropriate name in accordance with the rules of the International Code of Nomenclature.

19.4.2.1 How Many Rat Species in the Indochinese Region Are There?

According to Musser and Carleton (2005), nine genera comprising the following 27 species of Rattini may be encountered in our sampling area (Fig. 19.1): *Hapalomys delacouri*, *Sundamys muelleri*, *Chiromyscus chiropus*, three *Maxomys* species (*rajah*, *surifer*, *whiteheadi*), six *Niviventer* species (*fulvescens*, *hinpoon*, *langbianis*, *tenaster*, *cremoriventer*, *confucianus*), three *Leopoldamys* species (*neilli*, *edwardsi*, *sabanus*), two *Bandicota* species (*indica* and *savilei*), two *Berylmys* species (*bowersi* and *berdmorei*), and eight *Rattus* species (*andamanensis*, *argentiventer*, *exulans*, *tanezumi*, *losea*, *tiomanicus*, *norvegicus*, *nitidus*). According to our phylogeny (Fig. 19.1), 23 lineages exist within our sampling and 24 putative species were evidenced by the method of Pons *et al.* (2006). The estimated number of species fit well with the number of species described in the literature for this area, although there are some exceptions, in particular within the *Berylmys* and the *Rattus* genera. Our study suggests three putative species of *Berylmys* in our sampling, whereas only two are mentioned in the literature for the geographic area sampled (*B. bowersi* and *B. berdmorei*). This finding may be an artifact of the species delimitation method, which could have difficulties in dealing with high levels of population differentiation and strong phylogeographic patterns.

In a similar way, five species belonging to the *Rattus rattus* species group have been described in this area (i.e., *R. andamanensis*, *argentiventer*, *tanezumi*, *losea*, and *tiomanicus*). Our study confirms the presence of an additional *Rattus* species (labeled R3 in Fig. 19.2) already identified as the *diardii* clade in the mitochondrial phylogeny of Robins et al. (2007). R3 could be a cryptic species. Yet, this statement needs further investigation using independent data (morphology, nuclear genes) before taxonomic conclusions can be drawn (*R. diardii* is indeed considered at present as a synonym of *R. tanezumi*, Musser and Carleton 2005). In agreement with our result, Aplin et al. (2003b) in their preliminary study of the cytb gene observed that the taxonomy of the *Rattus rattus* species group might be rather more complex than suggested by previous studies mostly based on karyotypic or electrophoretic evidence. Indeed, his ongoing study mentions two distinct phylogenetic clades in the Asian region. The first one would correspond to an endemic South East Asian taxon (recorded in Vietnam, Cambodia, and Southern Laos) named *Rattus diardii* and might correspond to our R3 according to geographical evidence. Our study and Robins' work evidenced that the distribution of this South East group spreads far into the south as it occurs in Thailand and in Sri Lanka and also in Malaysia, in Indonesia, and Northern Sulawesi. The second clade proposed by Aplin et al. (2003b) would be a northern and South Asian taxon (found in Japan, Hong Kong, northern Vietnam, northern Laos, and Bangladesh) named *Rattus tanezumi* and might correspond to R2. Indeed, when including Robins' sequences, R2 includes specimens from Japan and Hong Kong. As mentioned by Aplin et al. (2003b), the latter group (R2) is more closely related to *Rattus rattus* rather than the former group (R3). In our trees (Figs. 19.1 and 19.2), R2 is clearly placed as the sister taxon of *R. rattus* (R1). Our study supports Aplin et al.'s (2003b) assumption that the two Asian clades (i.e. R2 and R3) are sympatric in some part of their distribution by increasing greatly the area where the two taxa co-occur in continental South East Asia. Both are found in Northern and Central Thailand (Phrae, Nakhon Pathom and Ratchaburi provinces; Pagès et al. 2010).

19.4.3 Phylogeographic Structure of Leopoldamys neilli

Our study evidenced a high geographic structure of the genetic diversity for *L. neilli*. Indeed, six different highly differentiated genetic lineages were observed. Each of them corresponds to particular regions of Thailand (Loei, Nan, Phrae, Saraburi-Nakhon Ratchasima, Lopburi, Kanchanaburi provinces) (see Fig. 19.4). The most differentiated lineage corresponds to the populations from the Kanchanaburi province (Western Thailand), which would have been separated for at least 1.8–2 million years from the other genetic lineages. It is interesting to note that this region was also characterized by a particular genetic lineage for the genus *Berylmys* (see above). Therefore, this last region seems to have been isolated from the other Thai regions following a still unknown historical or environmental event and this would have led to the appearance of different genetic lineages for the rodent communities living in this region. The study of other organisms coming from this area would be highly interesting to better estimate if this isolation can be generalized to other groups of animals or plants and to understand the reasons of this phenomenon.

The other lineages appear more related even if each of them is genetically differentiated and appears to be separated from the others for at least 1 million years. This result is surprising as these populations are sometimes geographically very close to each other (less than 30 km among the two genetic lineages observed in the Saraburi and Nakhon Ratchasima region. See Fig. 19.4).

Such high degree of genetic differentiation among the studied *L. neilli* populations could be explained by the following hypothesis:

Fig. 19.4 Geographic distribution of the different genetic lineages observed within *Leopoldamys neilli* in Thailand. With 1: Kanchanaburi; 2: Saraburi-Lopburi; 3: Saraburi-Nakhon Ratchasima; 4: Loei; 5: Phrae and 6: Nan provinces (modified from Latinne et al. 2011)

- The ancestor of *L. neilli* diverged from the other *Leopoldamys* species at the end of the Tertiary (2.75–3.5 million years ago). This differentiation would be associated to the important climate cooling which characterized this period and which led to the aridification of most tropical regions in the world (Hewitt 2000). This aridification had an important impact on the distribution of the tropical wet forests, which only survived in some patches and which were replaced in many other areas by colder and arid-adapted vegetation (Penny 2001; Hope et al. 2004). It was maybe during this period that *L. neilli* evolved to be more adapted to the dry vegetation presently characterizing its endemic limestone habitat (Waengsothorn 2007).

- Following the extension of dry forests during the cooling periods of the Early Quaternary (around 2.5–2 million years ago), *L. neilli* would have been able to colonize a large area including the majority of continental Thailand.

- Later, during the different warming periods characterizing the Quaternary era, the dry forests were replaced by wet tropical ones in many areas of Thailand (Hewitt 2000), probably with the exception of small spots like the limestone areas, which are characterized by particular substrates favoring dry vegetation. *L. neilli* populations would have been "trapped" in karst habitats during these periods (first, around 1.8–2 million years ago in the Kanchanaburi region; later, around 1 million years ago, in the other Thai limestone areas) where they diverged by allopatric differentiation. This phenomenon would have led to the highly differentiated genetic lineages presently observed within this species. High levels of intraspecies divergence have been observed in other taxa which are dependent on patchy habitat; for instance, Colorado springsnails and Iowa Pleistocene snails (Ross 1999; Hurt 2004), the mosquito, *Anopheles scanloni* (Loughlin et al. 2007), and the rodent *L. aenigmamus* (Rivière-Dobigny et al. 2010). The high levels of differentiation observed within these last species are also explained as being the results of allopatric fragmentations which appeared during the Quaternary climate changes.

19.4.3.1 Implications for the Taxonomy and the Conservation of *L. neilli*

Our study evidenced the existence of highly differentiated genetic lineages within *L. neilli* corresponding to different limestone regions spread all over Thailand. These populations are separated by a very high level of genetic divergence (between 4 and 7% K2P distance, see Table 19.2). These values correspond to what is generally observed at least among subspecies in other rodents (e.g., Bradley and Baker 2001; Michaux et al. 2003, 2005). Therefore, as the *L. neilli* genetic lineages are also geographically well isolated, they would be considered as distinct subspecies or at least as distinct Evolutionarily Significant Units (ESU) or Management Units (MU) (Avise 2000).

This information is extremely important for the conservation of *L. neilli*. Indeed, as the Thai limestone areas are characterized by particular endemic genetic lineages of this species and as they are presently highly threatened by quarrying, deforestation, hunting, and urbanization (Vermeulen and Whitten 1999; Clements 2006), it is very likely that each karst destruction will lead to the disappearance of unique intraspecific *L. neilli* lineages not found elsewhere in South East Asia. According to these data and as the distribution of this species appears very limited (some areas in Thailand and maybe in southern Laos) (Marshall 1977; Latinne and Michaux Personal Communication), we strongly suggest considering this species again as endangered on the IUCN Red List (Lunde and Aplin 2008).

These results also enhance the importance to conserve in priority the limestone habitats to preserve not only their huge interspecific (Clements et al. 2006; 2008), but also intraspecific biodiversity. The study of the genetic structure of other species endemic to this kind of habitat will allow to generalize this observation and to propose the best conservation measures for it.

19.5 Conclusions

This study represents the first step of a long-term project aiming to better understand the South East Asian rodent biodiversity.

From the interspecific point of view, our molecular study revealed a very high number of Rattini species in the Indochinese region, confirming the importance of South East Asia as a center of diversification of this rodent group. We notably found that at least six putatively different species, including a cryptic one (R3), could exist within the *Rattus rattus* species group (among which five were sampled within the area we investigated).

On the intraspecific level, our researches revealed an unexpectedly high level of genetic differentiation within the species *L. neilli*. Such a result is of major importance for the conservation of this threatened species as well as for a better understanding of the evolutionary processes that gave rise to the extreme rodent diversification in South East Asia.

In conclusion, our different results evidence that South East Asia might not only be a hotspot of interspecific but also of intraspecific biodiversity. In light of the extreme levels of species disappearance associated with the human pressures characterizing this region (habitat fragmentation and destruction, pollution, climate changes, hunting *this region should urgently manage its environment less aggressively*, to preserve, as long as it is still possible, this unique and fragile biological richness.

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Chapter 20
The Amphibians and Reptiles of Sulawesi: Underestimated Diversity in a Dynamic Environment

André Koch

Abstract Compared with the herpetofauna of the Sunda shelf islands, the diversity of amphibian and reptile genera on Sulawesi is impoverished. The oceanic character of the herpetofauna is the result of the million-year-long geographic isolation of Sulawesi which is separated from surrounding islands by deep ocean trenches. However, despite ambitious investigations by several industrious scientists during the past two centuries, recent fieldwork on Sulawesi and its smaller off-shore islands has revealed that the diversity of amphibians and reptiles has been largely underestimated. Since the last herpetological synopsis was published in 1996, 30 new amphibian and reptile species plus five subspecies have been described or newly recorded for Sulawesi and its satellite islands. In addition, more than 40 species, mainly skinks, have been identified as new to science and await formal description. This represents an increase by more than 35%! In total, about 210+ different species of amphibians and reptiles are currently recognized from the Sulawesi region almost 60% of which are endemics.

20.1 Sulawesi: An Island Between the Realms, but on Which Side of the Dividing Line?

Sulawesi, or Celebes as it was formerly known, lies right in the heart of the Indo-Australian Archipelago, the world's largest chain of islands bridging Asia and Australia. Crossed by the equator, Sulawesi is surrounded by Borneo to the west, the Philippines to the north, the Moluccas to the east, and the Lesser Sunda Islands to the south (Fig. 20.1). Only surpassed in size by the three Greater Sunda Islands and New Guinea, Sulawesi is the fifth largest island of Indonesia, one of the earth's

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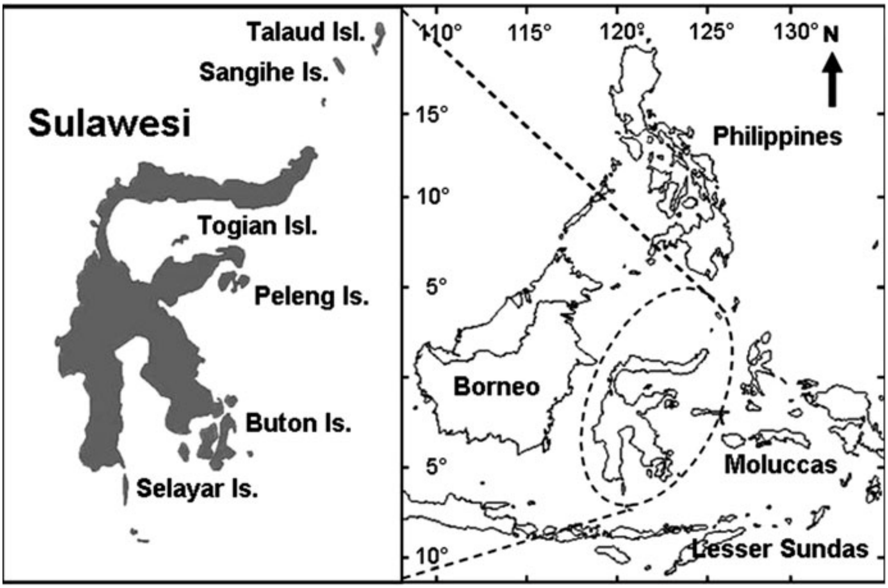

Fig. 20.1 Map of Sulawesi and its satellite islands in insular Southeast Asia

megadiversity countries (Mittermeier and Mittermeier 1997; Myers et al. 2000). The mountainous island is well known for its characteristic K-like shape composed of four peninsulas. It is naturally covered with pristine tropical rainforests.

Due to its exceptional topographic position between the Oriental and the Australian faunal realms, Sulawesi, together with the Lesser Sunda Islands and the Moluccas, represents a zoogeographic transition zone called Wallacea. Accordingly, Sulawesi's fauna comprises a unique assemblage of typical Asian (Oriental), and also Australo-Papuan species. Within Wallacea, Sulawesi and its smaller offshore islands form the so-called Sulawesi (sub-)region (Vane-Wright 1991).

However, compared to other large Indonesian islands such as Borneo, Sumatra or Java, Sulawesi's indigenous fauna is highly endemic and relatively poor in species. Among the non-volant mammals, for example, nearly 100% are endemic to Sulawesi (Groves 2001). With regard to invertebrates, Sulawesian butterflies show a low degree of generic endemism, but the level of species endemism is high suggesting a long but not excessive period of evolution in spatial isolation (Vane-Wright and de Jong 2003).

The oceanic character of the (herpeto)fauna is the result of the million-year-long geographic isolation of Sulawesi which is separated from surrounding islands by deep ocean trenches. These marine barriers impeded considerably the colonization of Sulawesi in the past. However, there have been several occasions for a faunal exchange between Sulawesi and neighboring island regions. Faunal migration through island hopping and over-water dispersal might have been facilitated by the repeated drop of global sea levels up to 160 m (Lambeck et al. 2002) during the Pleistocene climate oscillations about 2 Ma to 10,000 ya.

From Borneo, which lies on the edge of the Eurasian continental shelf, Sulawesi is separated by the Macassar Strait, a narrow but deep ocean trench, which prohibited the generation of new overland connections during lowered sea levels (Voris 2000). Consequently, this geological break also represents a more or less distinct faunal break. Alfred Russel Wallace (1823–1913), the founder of zoogeography, was one of the first who recognized this faunal break (Wallace 1860). This imaginary dividing line, subsequently called Wallace's line, runs through the Indo-Australian Archipelago in a north to south direction.

Despite its position east of Wallace's line, the biogeographic affinities of the herpetofauna of Sulawesi are predominantly Asian (Oriental) with minor Australo-Papuan influences (Boulenger 1897). Because this general distribution pattern was also observed in other animal groups, Wallace (1910) later himself revised his biogeographic dividing line and set it east of Sulawesi. Nevertheless, unknowingly Wallace had discovered the tectonic boundary of the Sunda shelf. Today, Wallace's line persists as the western border of the Wallacea transition zone between the Asian and Australian faunas (Moss and Wilson 1998).

20.2 Sulawesi, a Composite Island with a Complex Geological History

Models of reconstructing the geological evolution of Central Indonesia are essential to our understanding of the origin of its unique fauna because the present shape of Sulawesi is the result of the complicated geological history of the entire Indo-Australian Archipelago which, according to Heaney (1999), is the most tectonically complex region in the world.

Sulawesi is a composite island consisting of four different tectonic provinces or terranes. These distinct microcontinental blocks (paleo-islands) date back to the early Tertiary (60–40 Ma ago) when the Australian and the Eurasian tectonic plates collided (Hall 2002). The first terrane, which formed the eastern margin of Sundaland until the early Miocene, today forms the southwestern peninsula including the western part of Central Sulawesi and the neck of the northern arm. In contrast, part of Central Sulawesi and most of the southeastern peninsula are composed of Mesozoic rocks similar to those of the Australian margin. Independently, the eastern and the remaining parts of the northern peninsula of Sulawesi consist of volcanic and mainly accreted material formed at plate margins during the Cenozoic. For most of Sulawesi's history, however, the northern arm was submerged by shallow sea and became dry land only within the last 5 Ma years. In addition to the main island terranes, the microcontinental fragments of the Buton-Tukang Besi and Banggai-Sula archipelagos complete the geological setting of the Sulawesi region. These small island groups consist of Paleozoic and Mesozoic rocks with shallow and deep marine sediments of Papua-Australian affinities. Both these fragments collided with the eastern and southeastern arms of Sulawesi in the Middle and at the end of the Miocene, respectively (for details see Hall 1998, 2002). As a result of these far-reaching geological processes, Sulawesi finally got its present, strongly structured shape as recently as during the Pliocene 2–3 Ma ago, when the discrete and partly submarine terranes and paleo-islands that had not had contact to other landmasses for millions of years accreted (Hall 1998; Moss and Wilson 1998).

Its complex geological history, the humid and warm climate together with its topographic position at the interface between the continents of Asia and Australia render Sulawesi a global biodiversity hotspot of unique and bizarre creatures; most notably the famous babirusa (*Babyrousa babyrussa*) or “pig deer.” But also the amphibians and reptiles of Sulawesi bear some peculiarities such as the world’s longest snake, a reticulate python (*Python reticulatus*) measuring almost 10 m in length (Raven 1946; McWhirter 1985), and many species found nowhere else on earth.

20.3 Collectors and Contributors to the Herpetology of Sulawesi: A Historical Perspective

In terms of novel species descriptions and records, there are only few periods in the history of Sulawesi which were important for the exploration of the island’s herpetofaunal diversity.

Although several young European naturalists such as Heinrich Kuhl (1797–1821), Johan C. van Hasselt (1797–1823), Salomon Müller (1804–1863), and Heinrich C. Macklot (1799–1832) were sent out by the “Natuurkundige Comissie voor Nederlands-Indië” (Commission for the Study of the Natural Sciences of the Netherlands East Indies) to the Dutch overseas colonies as early as the 1820s in order to explore their diverse and exotic fauna and flora (Klaver 2007), systematic investigations in the herpetofauna of Sulawesi started only in the late 1850s, when Pieter Bleeker (1819–1878) traveled the Minahassa peninsula of Northern Sulawesi (Bleeker 1856). Subsequently, Bleeker (1856, 1857), an early outstanding Dutch student of Indonesia’s incredible biodiversity, reported about 25 amphibian and reptile species for the first time for Sulawesi. He also published the first checklist encompassing 47 different species (including five marine species). Bleeker (1860) provided an updated checklist enumerating 51 amphibian and terrestrial reptile species (Fig. 20.2). In addition, two endemic snake species, viz. *Oligodon waandersi* and *Gonyosoma jansenii*, were described by Bleeker (1858, 1860).

Since Bleeker’s significant contributions to Sulawesi’s herpetology, progress in the exploration of the herpetofauna stagnated again until Adolf B. Meyer

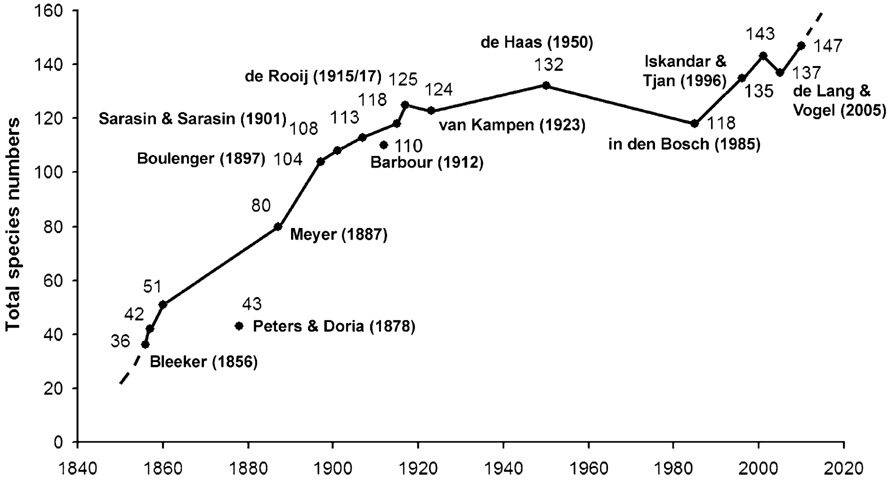

Fig. 20.2 Increasing total species numbers of Sulawesi's herpetofauna in a historical context. Shown are total numbers of described amphibian and reptile species either as reported by earlier authors (see e.g., Boulenger 1897) or as calculated from the respective group investigated (see e.g., in den Bosch 1985 for the snakes of Sulawesi) plus previously recorded species numbers of the remaining herpetofauna. Decreasing total numbers (see e.g., van Kampen 1923 or de Lang and Vogel 2005) are caused by the deletion of erroneous records from Sulawesi's species inventory

(1840–1911), a passionate ornithologist and later director of the Royal Museum for Natural History Dresden, Eastern Germany, visited Sulawesi in 1870 and 1873. Meyer's material formed the scientific foundation for numerous novel island records and species descriptions (see, e.g., Peters 1872a, b; Gray 1872; Günther 1873; Fischer 1880, 1882). Finally, Meyer (1887) listed a total of 80 amphibian and reptile species for Sulawesi and its satellite islands (Fig. 20.2).

Another European nation that sent out their naturalist explorers to the Indo-Malayan Archipelago was Italy. In 1874, the southeastern peninsula was the destination of a first expedition led by the naturalist Odoardo Beccari (1843–1920). The results of his collections were published by Doria (1874) and Peters and Doria (1878). All together, these authors listed 44 species of amphibians and reptiles for Sulawesi (Fig. 20.2). The endemics *Draco beccarii* and *Amphiesma celebicum* were described as novel species.

Another important phase began, when, between 1894 and 1897, numerous new species were described from Sulawesi based on the many voucher specimens collected by Paul (1856–1929) and "Fritz" Sarasin (1859–1942), two wealthy Swiss naturalists and explorers (Sarasin and Sarasin 1905). The herpetological results of their Sulawesi expeditions were initially published by "Fritz" Müller (1894). After Müller's death, George A. Boulenger (1858–1937) from the British Museum in London and Jean Roux (1876–1939), Müller's successor at the museum in Basel, continued to report on new collections made by the Sarasins (Boulenger 1896, 1897;

Roux 1904). Their collections represented 86 amphibian and reptile species, 18 of which proved to be new to science and 11 new to Sulawesi. In his systematic synopsis, Boulenger (1897) listed 104 different species (Fig. 20.2). He also pointed out the close zoogeographic affinities of the amphibians and reptiles of Sulawesi with the Greater Sunda Islands to the west (Boulenger 1897).

After the extensive expeditions by the Sarasins, only a few twentieth century herpetologists visited Sulawesi. During World War I, "Nelly" de Rooij (1883–1964), curator for herpetology at the Zoological Museum of Amsterdam, published a comprehensive two-volume work about "The Reptiles of the Indo-Australian Archipelago" (de Rooij 1915, 1917). Altogether, she treated in detail 101 different lizard and snake species for Sulawesi. In 1923, Pieter van Kampen (1878–1937) published "The Amphibia of the Indo-Australian Archipelago" to complete the work on the herpetofauna of the Dutch colonies in Southeast Asia (van Kampen 1923). He listed 23 different frog species for the Sulawesi region bringing the total number of amphibians and reptiles to 124 (Fig. 20.2). Before the outbreak of World War II, only a few more publications by Smith (1927), Ahl (1933) and Kopstein (1936) were devoted to the amphibians and reptiles of Sulawesi. These short contributions were virtually the last dealing exclusively with the extant herpetofauna of Sulawesi for the next 50 years.

After six decades of near ignorance, another period of enhanced systematic and taxonomic investigations started in the 1990s and still continues today (Fig. 20.3). These new surveys resulted in the most recent checklist of Sulawesi's entire herpetofauna by Iskandar and Tjan (1996). These authors listed a total of 135 described amphibian and reptile species for mainland Sulawesi and adjacent islands (Fig. 20.2). In addition, 20 species were assigned to as yet undescribed taxa.

In addition to these promising steps toward a comprehensive understanding of the amphibians and reptiles of Sulawesi, regional checklists about the herpetofauna of various off-shore islands were recently published (see Supriatna and Hedberg 1998: Talaud Islands, Gillespie et al. 2005: Buton Island, Koch et al. 2009b: Talaud Islands). Moreover, new subspecies (Auliya et al. 2002; Jacobs et al. 2009), new species (e.g., McCord et al. 1995; Brown et al. 2000; Orlov and Ryabov 2002; Howard and Gillespie 2007; McGuire et al. 2007; Hayden et al. 2008; Linkem et al. 2008; Koch et al. 2009c), and even new genera (in den Bosch and Ineich 1994: *Cyclotyphlops*, McCord et al. 2000: *Leucocephalon*) have been described on a regular basis. These recent additions to the herpetofauna of Sulawesi were supplemented by several new island records (e.g., Gillespie et al. 2005; Zug 2006; Koch et al. 2008).

However, despite two centuries of investigations, much remains to be done to achieve a complete species inventory of Sulawesi's diverse herpetofauna. Except for the snakes which have been reviewed by several authors within the last 100 years (see de Rooij 1917; de Haas 1950; in den Bosch 1985; de Lang and Vogel 2005), the herpetofauna of Sulawesi remains largely unknown and many new species await discovery and description.

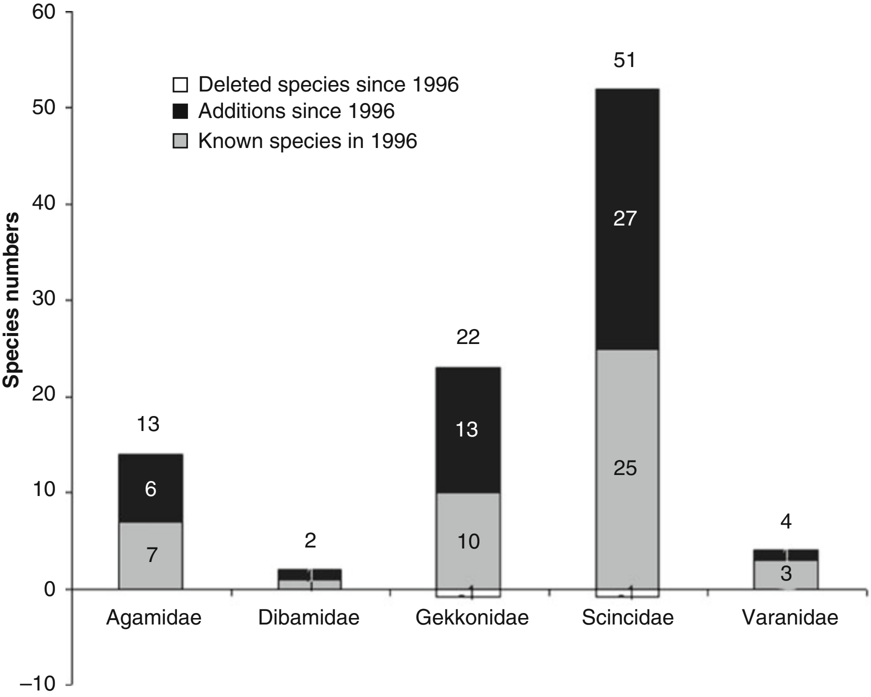

Fig. 20.3 Increase of species numbers for the five Sulawesi lizard families since 1996. Species numbers for geckos and skinks have doubled within the last 15 years. Together with colubrids, they make up nearly 70% of Sulawesi's entire reptile fauna

20.4 What Do We Know Today About the Herpetofaunal Diversity of Sulawesi?

20.4.1 Sulawesi's Amphibians: Poor in Species, but Highly Endemic

Compared to Sulawesi's diverse reptile fauna, amphibians constitute only about one-fourth of the island's herpetofaunal diversity. The frog fauna is spread over six families: Bufonidae, Ceratobatrachidae, Microhylidae, Ranidae, Hylidae, and Rhacophoridae.

Members of the genus *Bufo* are the only representatives of bufonids (Bufonidae) found on Sulawesi and adjacent islands. Only four species occur on Sulawesi, three of which are considered recent introductions to the fauna of Sulawesi (Iskandar and Tjan 1996). The family Ceratobatrachidae shows a disjunct distribution comprising Peninsular Malaysia, Borneo, the Philippines, New Guinea as well as the Bismarck, Admiralty, and Solomon Islands. It comprises five genera, one of which, viz. *Platymantis*, was recently found on Banggai Island within the Sulawesi region (Koch et al., unpublished), partly bridging the distribution gap of ceratobatrachid frogs. However, records from mainland Sulawesi are still missing. Microhylids are species-rich and nearly cosmopolitan in their distribution. Currently, eight species are recognized from the Sulawesi region. Of those, two species, viz. *Kaloula* sp. and *Oreophryne* sp., have been identified as new and await formal description (Iskandar and Tjan 1996; Gillespie et al. 2005). *Callulops* cf. *dubius*, representing a new genus and species record for the area, was only recently discovered on the Talaud Islands in the very north of the Sulawesi region (Koch et al. 2009b). Another new *Callulops* species is being described from Central Sulawesi (Iskandar et al. submitted). Ranidae are cosmopolitan frogs except for most of Australia, the West Indies, and the southern part of South America. Sulawesi ranids comprise 16 described species and at least 11 new species (Iskandar and Tjan 1996). Thus, Ranidae make up more than 50% of Sulawesi's amphibian fauna. Hylidae are a very diverse frog family. They are found throughout the Americas, the West Indies, Eurasia, northern Africa, and the Australo-Papuan region. Only one hylid frog, however, *Litoria infrafrenata*, is known from within the Sulawesi region. This Australo-Papuan species inhabits the Talaud Islands in the north of Sulawesi, where it reaches its most northerly distribution (Koch et al. 2009b). Rhacophorid frogs are mainly arboreal and include the flying frogs. From Sulawesi, five described species are known and two further species have been recognized as new (Iskandar and Tjan 1996). In addition, Gillespie et al. (2005) listed two species similar to *Rhacophorus monticola* from Buton Island. Tree frogs account for nearly 20% of Sulawesi's anuran diversity. They show a high degree of endemism (about 90%!).

In total, about 50 different frog species are currently recognized from Sulawesi, 20 of which (i.e., about 40%), however, are still undescribed or undetermined species (Fig. 20.4). Since the last synopsis was published in 1996, 11 new frog species (i.e., about 20% of the entire amphibian diversity of Sulawesi) have been newly recorded from this Central Indonesian island area (Table 20.1). In addition, the taxonomic status of some widespread species needs revision.

A high degree of endemism (>75%!) at the species level has been claimed for the indigenous amphibians of Sulawesi (Whitten et al. 2002). Only seven frog species are shared with Borneo according to Inger (2005). Of those, five frogs are considered obligate commensals of man (*Bufo melanostictus*, *Kaloula pulchra*, *Fejervarya limnocharis*, *Rana erythraea*, and *Polypedates leucomystax*), which could have easily been introduced into Sulawesi in the past. At the generic level, however, the frogs of Sulawesi are closely related to the Bornean-Malayan fauna, albeit much less diverse (Inger and Stuebing 2005).

In terms of amphibian diversity, Sulawesi is the least studied area compared to the larger neighboring islands of the Sunda shelf (Inger 2005; Iskandar 2008). In contrast to Sulawesi's reptiles, where new species are described on a regular basis (see Table 20.1), the last frog descriptions were published about 80 years ago in the late 1920s and early 1930s (see Smith 1927; Ahl 1933). The recent discoveries

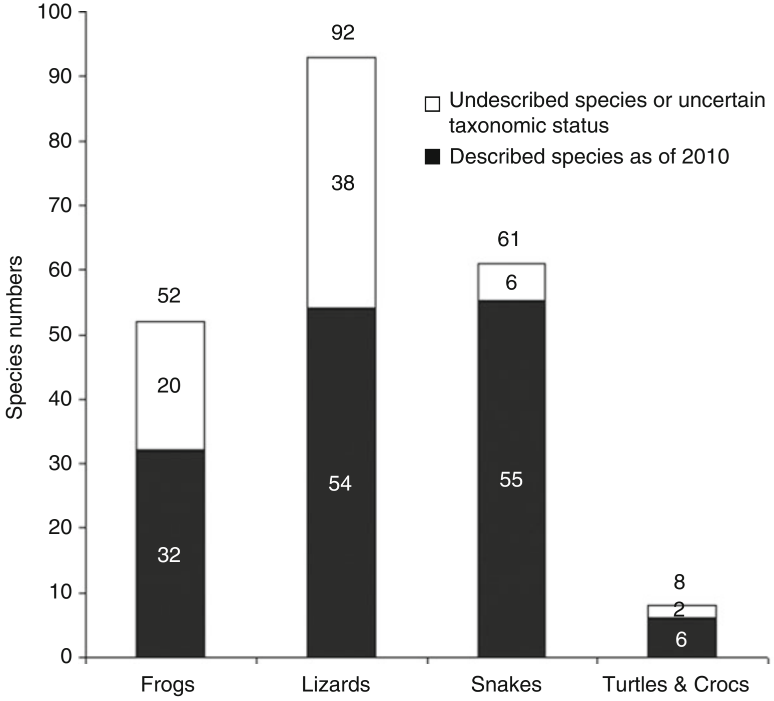

Fig. 20.4 Relation between described and undescribed or undetermined species of Sulawesi's herpetofauna. Note the high percentage of undescribed frogs and lizards (about 40%) as compared with snakes, turtles and crocodiles

of numerous new and undetermined frogs and toads (see, e.g., Iskandar et al. submitted; Iskandar and Tjan 1996; Koch et al. 2009b; Malkmus 2000) represent the beginning of a new era of amphibian descriptions from the Sulawesi region.

20.4.2 Sulawesi's Reptiles: Species-rich, but Only Partly Well Investigated

About three-fourth of the herpetofaunal diversity of Sulawesi are reptiles. Currently, they add up to 160 species in total. The majority of the reptile fauna, however, is composed of only few squamate groups. Two families, viz. Scincidae and Colubridae, together make up more than 50% of all Sulawesi reptile species! This dominance nearly reaches 70%, when the Gekkonidae are included (see Table 20.2). Of these three major reptile groups, 45 species (i.e., more than 40%) have been described, identified as new to science or newly recorded for the Sulawesi region within just the last 15 years (Fig. 20.3), when investigations into the herpetofauna of Sulawesi experienced a successful revival.

Table 20.1 Additions to the herpetofauna of Sulawesi and adjacent islands since the last checklist by Iskandar and Tjan (1996)

Species	Location	Status	References
Amphibians (11 spp.)			
Bufonidae (2 spp.)			
Bufo sp.	Sulawesi	NR/(US)	Malkmus (2000)
Bufo asper	Sulawesi	NR/I	Iskandar and Colijn (2000)
Microhylidae (3 spp.)			
Callulops cf. *dubius*	Talaud Ids.	NG/(US)	Koch et al. (2009a)
Callulops sp. n.	Sulawesi	NS	Iskandar et al. (submitted)
Oreophryne sp.	Buton Id. (endemic?)	US	Gillespie et al. (2005)
Ceratobatrachidae (1 sp.)			
Platymantis papuensis occidentalis	Banggai Id.	NG	Koch et al. (unpublished)
Ranidae (2 spp.)			
Rana everetti	Sulawesi	RV	Iskandar and Colijn (2000)
Limnonectes sp. n. (cf. *kuhlii*)	Sulawesi	US	Frost (2010)
Rhacophoridae (2 spp.)			
Rhacophorus cf. *monticola* 1	Buton Id.	US	Gillespie et al. (2005)
R. cf. *monticola* 2	Buton Id.	US	Gillespie et al. (2005)
Hylidae (1 sp.)			
Litoria infrafrenata	Talaud Ids.	OL	de Jong (1928)
Turtles and tortoises (3 spp.)			
Emydidae (1 sp.)			
Trachemys scripta elegans	Sulawesi	NG/I	Platt et al. 2001
Trionychidae (2 spp.)			
Amyda cartilaginea	Sulawesi	NG/(I)	Koch et al. (2008)
Pelochelys sp.	Sulawesi	NG/US	Webb (2002)
Lizards (51 spp.)			
Scincidae (29 spp.)			
Cryptoblepharus cursor larsonae	Sulawesi (endemic)	OL/NSS	Mertens (1934, 1964), Horner (2007)
Cryptoblepharus sp.	Togian Ids.	US	Supriatna and Hedberg (1998)
Emoia cf. *ruficauda*	Banggai Id.	NR/(US)	Koch et al. (unpublished)
Emoia sp. 1	Togian Ids.	US	Supriatna and Hedberg (1998)
Emoia sp. 2	Togian Ids.	US	Supriatna and Hedberg (1998)
Emoia sp. 3	Togian Ids.	US	Supriatna and Hedberg (1998)
Emoia sorex	Sulawesi	OL	Brown (1991)
Lamprolepis cf. *smaragdina*	Hoga Id. (endemic)	US	Gillespie et al. (2005)
Lamprolepis sp.n.	Buton Id. (endemic)	US	Gillespie et al. (2005)
Lamprolepis sp.n.	Kalaotoa Id. (endemic)	US	Koch et al. (unpublished)
Lamprolepis sp.n.	Talaud Ids.	US	Koch et al. (2009b)
Lamprolepis sp.n.	Togian Ids. (endemic)	US	Koch et al. (unpublished)

(continued)

Table 20.1 (continued)

Species	Location	Status	References
Lipinia noctua	Talaud Ids.	OL	de Jong (1928)
Eutropis grandis	Sulawesi (endemic)	NS	Howard et al. (2007)
Eutropis sp.1	Sulawesi	US	Wanger et al. (2009)
Eutropis sp.2	Sulawesi	US	Wanger et al. (2009)
Eutropis sp.3	Togian Ids.	US	Supriatna and Hedberg (1998)
Sphenomorphus celebensis	Sulawesi	OL	Müller (1894)
Sphenomorphus sp.n.1	Buton Id. (endemic?)	US	Gillespie et al. (2005)
Sphenomorphus sp.n.2	Buton Id. (endemic?)	US	Gillespie et al. (2005)
Sphenomorphus sp.n.3	Buton Id. (endemic?)	US	Gillespie et al. (2005)
Sphenomorphus sp.n.4	Sulawesi	US	Linkem et al. (unpublished)
Sphenomorphus sp.n.5	Sulawesi	US	Linkem et al. (unpublished)
Sphenomorphus sp.n.6	Sulawesi	US	Linkem et al. (unpublished)
Sphenomorphus sp.n.7	Sulawesi	US	Linkem et al. (unpublished)
Parvoscincus sp.1	Sulawesi (endemic)	NG/US	Wanger et al. (2009)
Parvoscincus sp.2	Sulawesi (endemic)	NG/US	Wanger et al. (2009)
Tropidophorus baconi	Sulawesi (endemic)	NS/RV	Hikida et al. (2003)
Dibamidae (1 sp.)			
Dibamus celebensis	Sulawesi (endemic)	RV	Schlegel (1858), Greer (1985)
Gekkonidae (13 spp.)			
Luperosaurus iskandari	Sulawesi (endemic)	NS/NG	Brown et al. (2000)
Hemiphyllodactylus typus	Sulawesi	NG	Gillespie et al. (2005)
Lepidodactylus aureolineatus	Sulawesi	NG/I	Zug (2006)
Cyrtodactylus wallacei	Sulawesi (endemic)	NS	Hayden et al. (2008)
C. spinosus	Sulawesi (endemic)	NS	Linkem et al. (2008)
Cyrtodactylus sp.1	Selayar Id.	US	Hayden et al. (2008)
Cyrtodactylus sp.2	Tanahjampea Id.	US	Hayden et al. (2008)
Cyrtodactylus sp.3	Togian Ids.	US	Supriatna and Hedberg (1998)
Cyrtodactylus sp.4	Togian Ids.	US	Supriatna and Hedberg (1998)
Cyrtodactylus sp.	Buton Id.	US	Gillespie et al. (2005)
Gehyra sp.	Buton Id.	US	Gillespie et al. (2005)
Gekko smithii	Sulawesi	NR/(I)	Koch et al. (2009d)
Nactus cf. *pelagicus*	Talaud Ids.	NG/US	Koch et al. (2009b)
Agamidae (6 spp.)			
Draco caerulhians	Sangihe Id. (endemic)	OL	Lazell (1992)
D. beccarii	Sulawesi (endemic)	RV	McGuire et al. (2007)
D. iskandari	Tahulandang Id. (endemic)	NS	McGuire et al. (2007)
D. rhytisma	Banggai Id. (endemic)	OL	Musters (1983)

(continued)

Table 20.1 (continued)

Species	Location	Status	References
D. supriatnai	Togians (endemic)	NS	McGuire et al. (2007)
Hypsilurus cf. *dilophus*	Sulawesi	NG/US	Manthey and Denzer (2006)
Varanidae (2 spp.)			
Varanus lirungensis	Talaud Ids. (endemic)	NS/RV	Koch et al. (2009c)
Varanus sp. n.	Banggai Id. (endemic)	US	Koch et al. (unpublished)
Snakes (10 spp. + 3 spp.)			
Pythonidae (3 spp.)			
Python reticulatus saputrai	Sulawesi (endemic)	NSS	Auliya et al. (2002)
P. reticulatus jampeanus	Tanahjampea Id. (endemic)	NSS	Auliya et al. (2002)
Python bivittatus progschai	Sulawesi (endemic)	NSS/RV	Jacobs et al. (2009)
Viperidae (1 sp.)			
Tropidolaemus laticinctus	Sulawesi (endemic)	NS	Kuch et al. (2007)
Colubridae (5 spp.)			
Boiga tanahjampeana	Tanahjampea Id. (endemic)	NS	Orlov and Ryabov (2002)
Calamaria longirostris	Buton Id. (endemic)	NS	Howard and Gillespie (2007)
C. butonensis	Buton Id. (endemic)	NS	Howard and Gillespie (2007)
C. banggaiensis	Banggai Id. (endemic)	NS	Koch et al. (2009a)
Dendrelaphis marenae	Sulawesi	NS/RV	Vogel and van Rooijen (2008)
Typhlopidae (1 gen., 3 spp.)			
Cyclotyphlops deharvengi	Sulawesi (endemic)	NS/NG/OL	in den Bosch and Ineich (1994), Gillespie et al. (2005)
Typhlops sp. 1	Talaud Ids. (endemic?)	US	Koch et al. (2009b)
Typhlops sp. 2	Buton Id. (endemic?)	US	Gillespie et al. (2005)
Boidae (1 spp.)			
Candoia paulsoni tasmai	Talaud Ids.	NSS/RV	Smith and Tepedelen in Smith et al. (2001)

NR new species record, *NG* new genus record, *NS* new species, *NSS* new subspecies, *I* introduced species, *OL* overlooked by Iskandar and Tjan (1996), *US* undescribed or undetermined species, *RV* re-described or revalidated taxa

20.4.2.1 Squamates

The Lizard Fauna: Highly Diverse, but Often Undescribed

On a global scale, lizards are the most diverse group of extant reptiles. Also on Sulawesi, lizards represent the most species-rich reptile group. Until today, more

Table 20.2 Summary of Sulawesi's herpetofaunal diversity at family level

Families (*n*)	Described species	Undescribed species	Uncertain status	In total	% Undescribed or uncertain status
Frogs (6)					
Bufonidae	4	0	1	5	20
Ceratobatrachidae	1	0	0	1	0
Microhylidae	5	3	1	9	44
Ranidae	16	11	0	27	41
Hylidae	1	0	0	1	0
Rhacophoridae	5	2	2	9	44
Total	**32**	**16**	**4**	**52**	**38**
Lizards (5)					
Agamidae	10	0	3	13	23
Dibamidae	2	0	0	2	0
Gekkonidae	15	4	3	22	32
Scincidae	24	20	7	51	53
Varanidae	3	1	0	4	25
Total	**54**	**25**	**13**	**92**	**41**
Turtles (4)					
Emydidae	1	0	0	1	0
Geoemydidae	2	0	0	2	0
Testudinidae	1	0	0	1	0
Trionychidae	1	0	1	2	50
Total	**5**	**0**	**1**	**6**	**17**
Crocodiles (1)					
Crocodylidae	1	0	1	2	50
Snakes (10)					
Acrochordidae	1	0	0	1	0
Boidae	2	0	0	2	0
Colubridae	34	0	1	35	3
Cylindrophiidae	3	0	1	4	25
Elapidae	1	0	0	1	0
Homalopsidae	3	2	0	5	40
Pythonidae	2	0	0	2	0
Typhlopidae	5	1	1	7	29
Viperidae	3	0	0	3	0
Xenopeltidae	1	0	0	1	0
Total	**55**	**3**	**3**	**61**	**10**
Reptiles total	**115**	**28**	**18**	**161**	**29**
Herpetofauna total	**147**	**44**	**22**	**213**	**31**

Note the high number of undescribed species for some amphibian and lizard families. The systematic used here follows the higher taxa groupings by Frost (2010) for amphibians, by Uetz (2009) for squamates, and by Fritz and Havaš (2007) for turtles

than 90 different species have been identified. The lizard diversity is assignable to five different families: Agamidae, Dibamidae, Gekkonidae, Scincidae, and Varanidae.

Within the herpetofauna of Sulawesi, the skinks (Scincidae) are the largest family of all reptiles. About 50 different species belonging to 11 genera are recognized (Fig. 20.3). The genus *Parvoscincus* was only recently recorded for Central Sulawesi (Wanger et al. 2009). Skinks represent about 55% of the lizard fauna, followed by the geckos, which comprise one-fourth of Sulawesi's lizard diversity. The enormous number of 27 new skink species (i.e., more than 50% of the entire skink fauna) has been identified since 1996 (Table 20.1). However, nearly the same number of skink species represents new or unidentified species. In recent years, only two new skink species, viz. *Tropidophorus baconi* and *Eutropis grandis*, have been described from Sulawesi (Hikida et al. 2003; Howard et al. 2007). For the large genus *Sphenomorphus* alone, which already comprises more than one-third of Sulawesi's skink diversity with nine recognized species, another nine new species await formal description (C. W. Linkem, personal communication).

Surpassed only by skink diversity, geckos (Gekkonidae) represent the second largest lizard group on Sulawesi. At present, about 20 different gecko species spread over nine genera are known from Sulawesi and its off-shore islands. Thirteen gecko species including three genera have been added to the herpetofauna of Sulawesi within the last 10 years alone (Fig. 20.3). Three turned out to represent novel species, while four geckos were recorded for the first time for Sulawesi. Among these new island records is *Gekko smithii* (Koch et al. 2009d), one of the largest gecko species of Southeast Asia. Altogether, 60% of Sulawesi's gecko species have been described or recorded since 1996. This high percentage can only partly be explained by overlooking rare or cryptic species such as *Luperosaurus*. The discoveries of the large-bodied *G. smithii* and other species rather suggest that this lizard group has been largely neglected by herpetologists in the past.

With four described endemic species, the genus *Cyrtodactylus* comprises almost 20% of Sulawesi's gecko fauna, but this percentage may increase up to 40% in the future because at least three new species of this genus have already been identified. The taxonomic status of two undetermined *Cyrtodactylus* species from the Togian Islands (Supriatna and Hedberg 1998), Central Sulawesi, remains unclear. In addition, one new *Gehyra* from Buton has been recorded (Gillespie et al. 2005). The degree of endemism among Sulawesi gecko species is about 50%.

Currently, 13 agamid species (Agamidae) are known to inhabit the Sulawesi region (Fig. 20.3). With eight described species, flying lizards of the genus *Draco* comprise 60% of all Sulawesi agamids. They show a high degree of local endemism (McGuire et al. 2007). In contrast, the agamid genus *Hydrosaurus* is represented by only one large species, *H. amboinensis*. The taxonomic status of the Sulawesi population, however, deserves further investigation. Recently, Manthey and Denzer (2006) reported on a photographic record of *Hypsilurus* cf. *dilophus* from Sulawesi. As this agamid species is only known from New Guinea, the Sulawesi record requires verification.

Blind lizards (Dibamidae) of the genus *Dibamus* were long considered poor in species, with *D. novaeguineae* being the only recognized representative (de Rooij 1915). Traditionally, Sulawesi specimens have also been assigned to this species. Greer (1985), however, showed that this island population actually represents two distinct species, viz. *D. novaeguineae* and *D. celebensis*, which live in sympatry on Sulawesi.

Sulawesi is inhabited by two distinct endemic monitor lizard species (Varanidae) of the widespread *Varanus salvator* complex (Koch et al. 2007). Recent field work revealed that the diversity of Sulawesi monitor lizards is underestimated, particularly when the smaller off-shore islands are included. In addition, *V. lirungensis*, a new member of the *V. indicus* species group, was described from the Talaud Islands in the very north of Sulawesi (Koch et al. 2009c).

In sum, 49 lizard species (i.e., almost 50% of the entire lizard fauna of Sulawesi) have been documented and described within the last 15 years (Table 20.1) although a large percentage (about 40% representing 37 species) of the lizard fauna is not yet described or is of uncertain taxonomic status (Table 20.2).

Sulawesi's Snakes: Well Recorded and Understood

Though less rich in species compared to lizards, Sulawesi's snakes exhibit a higher diversity at genus level. In total, 61 snake species (excluding sea snakes) are currently recognized from Sulawesi. They are represented by ten different families, twice as many as lizard families. These are the Acrochordidae, Boidae, Colubridae, Cylindrophiidae, Elapidae, Homalopsidae, Pythonidae, Typhlopidae, Viperidae, and Xenopeltidae.

Nearly 60% of the snake species found on Sulawesi belongs to the Colubridae. Colubrids are the largest group of snakes worldwide. This paraphyletic family includes about two-thirds of all snake species. Consequently, colubrids also account for most of Sulawesi's snake diversity, where they occur in 17 different genera. The most species-rich colubrid genus of Sulawesi is *Calamaria* with 11 described species. Thus, *Calamaria* species make up nearly 20% of Sulawesi's snake diversity. Three endemic *Calamaria* species were only recently discovered (Howard and Gillespie 2007; Koch et al. 2009a). Altogether, the degree of endemicity of the genus *Calamaria* on Sulawesi exceeds 90%! Only one species, the widespread *C. virgulata*, is not restricted to the Sulawesi region. Thus, Sulawesi seems to have been the place for a minor radiation of these fossorial snakes and further taxa may be described in the future (see de Lang and Vogel 2005). File snakes of the family Acrochordidae are found from South and Southeast Asia through Indonesia, the Philippines, and New Guinea to northern Australia. One species, *Acrochordus granulatus*, inhabits Sulawesi. The species is found along the coastline in estuarine habitats and mangroves. In den Bosch (1985) expected a second species, *A. javanicus*, to co-occur on Sulawesi with *A. granulatus*. This species, however, has never been recorded there. On a global scale, boas (Boidae) inhabit a disjunct range from western North America to South America and the Caribbean, from Africa and Madagascar to southern Asia, and from eastern Indonesia to the Solomon Islands. Only the genus *Candoia*, the Pacific boas, is found on small satellite islands of northern Sulawesi with two distinct species. Records from mainland Sulawesi are most probably incorrect (Koch et al. 2009b). The Cylindrophiidae are a monotypic snake family which contains only the genus *Cylindrophis*. Currently, about ten different species are recognized from South and Southeast Asia as far east as the Aru Islands. Three species of cylindrophiid snakes are known from the Sulawesi region. Elapids are a family of venomous snakes with a worldwide distribution in the tropics and subtropics. Sulawesi is home to only one elapid snake. This, however, is the largest venomous snake in the world, the king cobra (*Ophiophagus hannah*), which can grow up to six meters. A second cobra species, *Naja sputatrix* from Java, has been recorded from Sulawesi with a single specimen (Kopstein 1936). This record, however, is doubtful and needs confirmation (de Lang and Vogel 2005). Currently, three species of homalopsine snakes (Homalopsidae) of the genera *Cerberus* and *Enhydris* are known from Sulawesi (de Lang and Vogel 2005). In addition, two undescribed species have been identified (Iskandar and Tjan 1996; Iskandar and Colijn 2001), one of which from Lake Towuti in Central Sulawesi is even considered to represent a new homalopsine genus (D. T. Iskandar, personal communication in de Lang and Vogel 2005). The second new species has been found near Mount Lompobatang on the southwestern peninsula (D. T. Iskandar, personal communication in de Lang and Vogel 2005). Pythons (Pythonidae) are large-bodied, non-venomous snakes that are distributed across Africa, Asia, and Australia. Among the Asian representatives that also inhabit Sulawesi is one of the longest snakes of the world, *P. reticulatus*. Altogether, two python species with three recently described endemic subspecies inhabit the Sulawesi region (Auliya et al. 2002; Jacobs et al. 2009). Blind snakes (Typhlopidae) are cosmopolitan, fossorial, and mainly small snakes. Five species are currently known from Sulawesi. Two further undescribed or undetermined species were recently reported from the islands of Buton (Gillespie et al. 2005) and Talaud (Koch et al. 2009b). The recently described genus *Cyclotyphlops* and *Typhlops conradi* are endemic to Sulawesi (in den Bosch and Ineich 1994). Vipers (Viperidae) have a worldwide distribution but are missing in Papua-Australia and many Pacific islands. On Sulawesi and its off-shore islands three species occur. *Trimeresurus fasciatus* is endemic to Tanahjampea Island. While the red-banded color morph of *Tropidolaemus* was only recently described as a new species, *T. laticinctus* (Kuch et al. 2007), the taxonomic status of the green-colored populations of Sulawesi is still under investigation. The monotypic family Xenopeltidae consists of only two harmless species, one of which, the widespread *Xenopeltis unicolor*, also occurs on Sulawesi.

Since 1996, ten new snake species plus three endemic subspecies have been identified or described from Sulawesi and its satellite islands (see Table 20.1). Thus, nearly 20% of the snake fauna of Sulawesi was recorded within the last 15 years. Only a minor percentage (about 10%) is still undescribed or unidentified today (Fig. 20.4). One of these novel snake species has been encountered near Lake Towuti in Central Sulawesi and probably represents a new homalopsine genus (see above). In sum, 36 snake species or almost 60% are endemics. At the genus level, three snake genera (i.e., nearly 10%) are considered endemic to Sulawesi. These are

Rabdion, *Cyclotyphlops* and the undescribed homalopsine genus. Hence, of the entire island herpetofauna, Sulawesi's snake diversity seems best studied and understood.

20.4.2.2 Turtles and Crocodiles: Exciting Recent Discoveries in Relict Reptiles

With six recognized non-marine species, turtles and tortoises form the smallest group of Sulawesi's herpetofauna together with the crocodiles. Sulawesi turtles belong to the families Emydidae, Geoemydidae, Testudinidae, and Trionychidae.

Due to their colorful patterns, sliders and allies (Emydidae) from North America have a long tradition in the international pet trade. One emydid turtle, the invasive *Trachemys scripta elegans*, has recently been introduced to Sulawesi (Platt et al. 2001). The predominantly Asian turtles of the family Geoemydidae also include the Sulawesian genera *Cuora* and *Leucocephalon*. *Leucocephalon yuwonoi* is the only recognized member of the endemic turtle genus *Leucocephalon* and was discovered through the US pet trade as recently as the early 1990s (McCord et al. 1995, 2000). About 50 species of Testudinidae are currently recognized. These herbivorous or omnivorous land tortoises are mainly found in Africa and Asia, and also in the Americas and Europe. Only one genus of extant land tortoise, *Indotestudo*, represented by the endemic *I. forstenii*, inhabits Sulawesi. Softshell turtles of the family Trionychidae comprise about 30 species worldwide. Only recently, the first record of the softshell turtle *Amyda cartilaginea* on Sulawesi was documented (Koch et al. 2008). This Asiatic softshell turtle was probably introduced by Chinese people for human consumption. In addition, an unconfirmed record of the trionychid genus *Pelochelys* from Sulawesi was published by Webb (2002).

Although turtles are medium to large-sized reptiles, the species diversity on Sulawesi has been doubled within the last 10 years! This high percentage of new species records is partly explainable by recent anthropogenic introductions as discussed for the softshell turtle *Amyda cartilaginea* or the invasive *Trachemys scripta elegans* (Koch et al. 2008). On the other hand, the description of *Leucocephalon yuwonoi*, an island endemic, as recently as 1995, and the unclear taxonomic status of *Pelochelys* softshell turtles, which were recorded for Sulawesi for the first time in 2002, demonstrate the consequences of decade-long neglect and insufficient knowledge about the amphibian and reptile diversity of Sulawesi.

Likewise, the number of crocodile species inhabiting Sulawesi and their taxonomic status are unclear. While up to five different species have been suggested to occur on Sulawesi (Platt et al. 2007), only two (i.e., *Crocodylus porosus* and a second, hitherto undetermined species) have been observed. Field surveys are urgently needed to clarify the distribution, taxonomy, and population status of Sulawesi crocodiles which are highly threatened by habitat destruction and the reptile leather trade.

20.5 Conclusions

20.5.1 Sulawesi's Herpetofaunal Diversity Has Been Underestimated

Despite the two-century-long investigations of several industrious scientists, much remains to be done to achieve a complete species inventory of Sulawesi's diverse herpetofauna. Today, the snakes are probably best understood, while the neglected amphibian and lizard diversity of Sulawesi is in severe need of taxonomic investigations (Fig. 20.4). Particularly, the rainforests of the mountainous interior of Central Sulawesi and some little explored off-shore islands may still harbor many undiscovered species.

Compared to the last checklist of Sulawesi's herpetofauna by Iskandar and Tjan (1996), 15 years later the total number of species has increased by more than 35%. Since 1996, 77 amphibian and reptile taxa including five subspecies have been added to the herpetofaunal inventory of Sulawesi and its smaller off-shore islands (Table 20.1). Of these, 18 species were recognized as new to science, 18 represented new island records, and seven taxa have been re-described or revalidated. Nine species have been overlooked in the past and 12 species, mainly snakes, were deleted from Sulawesi's species inventory. A total of 11 amphibian and reptile genera have been recorded from the Sulawesi region for the first time within the last 15 years. Three of these new genera, viz. *Leucocephalon*, *Cyclotyphlops* and an undescribed genus of homalopsine snakes, are even considered endemic to Sulawesi. The majority of these new species (i.e., more than 50% representing about 40 species), however, still remain undescribed or in need of taxonomic identification (Fig. 20.4).

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Chapter 21
The Brazilian Atlantic Forest: A Shrinking Biodiversity Hotspot

Milton Cezar Ribeiro, Alexandre Camargo Martensen, Jean Paul Metzger, Marcelo Tabarelli, Fábio Scarano, and Marie-Josee Fortin

Abstract The Neotropical Atlantic Forest is one of the world's top biodiversity hotspot. Originally, the forest extended over 1.5 million km^2 along the South American Atlantic coast, covering tropical and subtropical climates across highly heterogeneous relief conditions, which led to outstanding levels of endemism and species richness. Unfortunately, the Atlantic Forest has been historically altered by

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humans, which has resulted in severe habitat loss and fragmentation. The forest cover is now reduced to around 12% of its original extent, including regenerating areas and degraded forests, which are mostly spread in small fragments. As a result, many species are currently threatened to global extinction, with populations collapsing on local and regional scales. In this chapter, we reviewed the state of the art of Atlantic Forest biodiversity knowledge, pointing out the main achievements obtained by several research groups during the last decades. Additionally, we (1) propose a new sub-division of biogeographical sub-regions into 55 sectors considering 2,650 sub-watersheds, using niche theory and bioclimatic data; (2) describe the original and present distribution of the Atlantic Forest; and (3) relate the forest distribution to elevation and geomorphometric information (aspect and terrain orientation). Forest protection and restoration efforts, and potential ecosystem services are also examined as key topics driving the future of the Atlantic Forest biodiversity.

21.1 Introduction

The Atlantic Forest is the second largest rain forest of South America, once covering around 1.5 million km along the Brazilian coast, and extended westward into smaller, inland areas of Paraguay and Argentina (Galindo-Leal and Câmara 2003; Ribeiro et al. 2009). Stretching over extensive latitudinal (3°S to 30°S), longitudinal (35°W to 60°W), altitudinal (0–2,900 m asl), and soil-climatic gradients (e.g., 1,000–4,200 mm annual rainfall), Atlantic Forest is in fact extremely heterogeneous and encompasses large blocks of evergreen to semi-deciduous forests (the bulk of Atlantic Forest), but also deciduous forests, mangroves, swamps, *restingas* (coastal forest and scrub on sandy soils), inselbergs, high-altitude grasslands (*campo rupestre* and *campo de altitude*), and mixed *Araucaria* pine forests (Scarano 2002; Câmara 2003). This diversified mosaic of habitats is currently home of nearly 20,000 species of plants, 263 mammals, 936 birds, 306 reptiles, and 475 amphibians (Mittermeier et al. 2005). Moreover, outstanding levels of endemism make the Atlantic Forest one of the most distinctive biogeographic unit in the entire Neotropical Region (Müller 1973; Prance 1982).

The evolutionary history of the Atlantic Forest has been marked by periods of connection with other South American forests (e.g., the Amazon and Andean forests), resulting in biotic interchange, followed by periods of isolation that led to allopatric speciation (Silva et al. 2004). As a consequence, its biota is composed of both old (pre-Pliocene) and young (Pleistocene-Holocene) species (Silva and Casteleti 2003), which probably evolved within forest refuges that persisted in isolation during periods of drier climates (Silva et al. 2004). Such dynamic evolutionary history produced a very distinct biota consisting of five well-defined species centers (Silva and Casteleti 2003), with endemism rates ranging from 30% in birds to 44% in plants (Mittermeier et al. 2005).

Despite its extraordinary biodiversity and high levels of endemism, the Atlantic Forest has long experienced relentless habitat loss since the arrival of European colonists in the sixteenth century. A massive agricultural expansion in the colonial period, followed by industrialization and urban development, have profoundly affected the Atlantic Forest, which is now confined to only ~11.7% (163,377 km^2) of its original extent in Brazil (Ribeiro et al. 2009, hereafter, original will refer to pre-European period), 24.9% (11,618 km^2) in Paraguay (Cartes and Yanosky 2003; Huang et al. 2007, 2009), and ~38.7% (9,950 km^2) in northern Argentina (Chebez and Hilgert 2003; De Angelo 2009), so that 12.59% of the Neotropical Atlantic Forest remain today. Furthermore, habitat loss has reached more than 90% in some centers of endemism (Ribeiro et al. 2009), making the Atlantic Forest a global priority for biodiversity conservation, i.e., a biodiversity hotspot sensu Mittermeier et al. (2005). Overall, the Atlantic Forest has been converted into human modified or anthropogenic landscapes, which are typically agromosaics with a dynamic combination of small old growth forest remnants, early to late secondary forest patches on abandoned cropland or pasture, small patches of assisted regenerating forests, agroforestry patches, and plantations of exotic trees such as *Pinus* and *Eucalyptus*. Forest clearing is frequently associated with other human disturbances (e.g., hunting, logging, collection of non timber forest products), which has driven a fraction of the Atlantic Forest's unique biodiversity to nearly complete extinction (Tabarelli et al. 2005). In fact, few tropical biodiversity hotspots are "hotter" than the Atlantic Forest in terms of both existing threats and conservation value (Laurance 2009), despite its 700 protected areas (Galindo-Leal and Câmara 2003), which however protect only 1.62% of the region (Ribeiro et al. 2009).

In this chapter, we first document the environmental variability across the Atlantic Forest region, in order to better delimitate the bioclimatic distribution along its original extent. We overlapped bioclimatic data and the biogeographical sub-regions (Silva and Casteleti 2003) and proposed a refined new sub-division considering environmental variability within its 2,650 subwatersheds. Land use and historical and current habitat cover is examined at the biome scale in terms of both ecological/geographical distribution and landscape structure. We analyze the historical and present relationship between elevation and geomorphometric parameters (terrain orientation) and forest distribution. Forest conservation efforts, including Brazilian environmental legislation, are summarized, as well as key topics regarding ecosystem services and forest restoration. Finally, we examine potential perspectives, threats, and opportunities for Atlantic Forest conservation, and offer some general insights into the prospects for the persistence of biodiversity in human modified tropical forest landscapes worldwide.

21.2 Refinement of Biogeographical Sub-regions Using Bioclimatic Data

To characterize the Atlantic Forest region and refine the already well established biogeographical division of the Atlantic Forest (Silva and Casteleti 2003), we used bioclimatic and elevation data. Using data on birds, butterflies, and primates distributions, Silva and Casteleti (2003) proposed the partition of Atlantic Forest into eight biogeographical sub-regions (hereafter BSR), five as centers of endemism (Bahia, Brejos Nordestinos, Pernambuco, Diamantina, and Serra do Mar) and three as transition zones (São Francisco, Araucaria, and Interior Forests; see Fig. 21.1). Although this sub-division documents the major patterns of biodiversity distribution, with clear consequences for conservation planning, here we advocate for its refinement.

Humboldt and Bonpland (1807) recognized the importance of climate on species and biodiversity distribution, which later on, merged with the ecological niche concept (Grinnell 1917) defined as the range of ecological conditions under which a

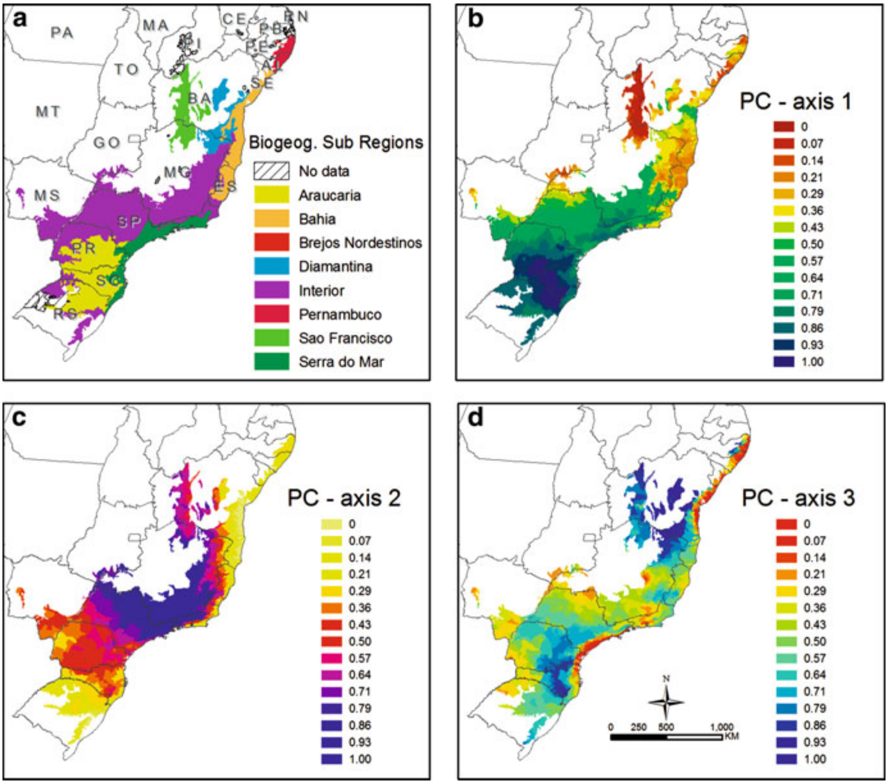

Fig. 21.1 (**a**) Biogeographical subregions (BSRs) proposed by Silva and Castelletti (2003); (**b**), (**c**), and (**d**) are PC axes obtained from the analysis of 19 layers from Worldclim 1.4 and an elevation map. Axis 1 (**b**) was mainly correlated with annual mean temperature and mean temperature in the coldest quarter; the warmer colors represent higher annual mean temperatures. Axis 2 (**c**) was more influenced by elevation, precipitation in the wettest month, precipitation seasonality, and precipitation in the wettest quarter; the cooler (*bluer*) colors indicate higher elevations, while *yellow* represents the lower elevations. Axis 3 (**d**) was mainly correlated with annual precipitation and precipitation in the warmest quarter; *warmer colors* represent higher annual precipitation, and *cooler colors* represent lower annual precipitation

species can occur spatially. Hutchinson (1957) clarified how species and environment are interrelated, using his multi-dimensional "hyper-volume" theory. Specifically, his concept merged autecology and predictive geographical modeling. Ecological niche models basically depict the relationship between species records and a set of environmental conditions, building mechanistic models that allow the extrapolation of potential biodiversity patterns and species occurrences (Guisan and Zimmermann 2000; Guisan and Thuiller 2005).

Environmental or spatial subdivisions can be determined at different spatial and temporal scales (Fortin and Dale 2005; Wagner and Fortin 2005). For macro-regional (>1 million ha) and continental scales, several datasets are now freely available from the Internet, particularly bioclimatic information. The most commonly used database is WORDCLIM 1.4 (http://biogeog.berkeley.eu, Hijmans et al. 2005; Ramirez and Jarvis 2008), which covers the entire globe with a ~900 m spatial resolution. Although the main applications of these map databases are in modeling species distributions, we used the bioclimatic information to refine the biogeographical divisions of the Atlantic Forest. We searched for a unique congruence of climate conditions that could disclose some particular environmental circumstance that might be distinct within the biogeographical region. Based on the results, we proposed to fine tune the Atlantic Forest subdivision.

21.2.1 Proposed Subdivision for BSRs

We used 19 environmental layers of WORDCLIM 1.4 (Hijmans et al. 2005; Ramirez and Jarvis 2008), and an elevation map to characterize the environmental niche amplitude of the region, as was previously used to model species distribution in the Atlantic Forest (Durães and Loiselle 2004; Acosta 2008; Torres et al. 2008; Murray-Smith et al. 2009; Fernandez et al. 2009; Marcelino et al. 2009; Siqueira et al. 2009; Loiselle et al. 2010). However, due to the high colinearity between the environmental and elevation variables, we conducted a PCA analysis to reduce dimensionality (for details of the method, see Loiselle et al. 2010). The first four PCA axes accounted for 92% of the variance, with the first two axes covering 71%. Axis 1 was mainly correlated with the annual mean temperature and the mean temperature in the coldest quarter of the year, while axis 2 was more influenced by elevation, precipitation in the wettest month, precipitation seasonality, and precipitation in the wettest quarter. Axes 3 and 4 (accounting for 21% of the explained variance) were mainly correlated with annual precipitation, precipitation in the warmest quarter, and the annual temperature range.

To map different environmental gradients (see Fig. 21.1b–d for Principal Components – PCs 1, 2, and 3, respectively), we plotted the bioclimatic derived PCA axis on a fifth-order subwatershed division (hereafter SWS; Pfastetter 1987). The SWS were selected because they allowed us to divide the entire Atlantic Forest into ~2,650 parcels, with a size ranging widely between the extremes of fine size for modeling and management (38% are <10,000 ha, and 60% <50,000 ha). Few SWS

($n = 25$) are >500,000 ha in size. The most common sizes of SWS (<50,000 ha) are ideal for regional planning, mainly because they allow the incorporation of landscape level features that are important for conservation and restoration planning. Moreover, the SWS units have been adopted by several Brazilian national agencies (ANA, IBAMA, and EMBRAPA) as the base unit for regional analysis and strategic planning. Therefore, we superimposed the SWS with PC axes on the BSRs proposed by Silva and Casteleti (2003), and produced scatter-plots of paired PC1–PC4. Although the BSRs can be clearly identified as forming groups, Fig. 21.2 shows that there is considerable overlap between the analyzed BSRs on the bioclimatic (PCs) space.

Because our objective in this analysis was to generate a more detailed sub-division of the Atlantic Forest, we combined a cluster analysis with the BSRs suggested by Silva and Casteleti (2003). The results of this superposition are shown in Fig. 21.3. We divided the Atlantic Forest into 55 small sectors, and the number of divisions was proportional to the sizes of the BSR (Table 21.1), which means that the BSRs contain similar heterogeneity within them.

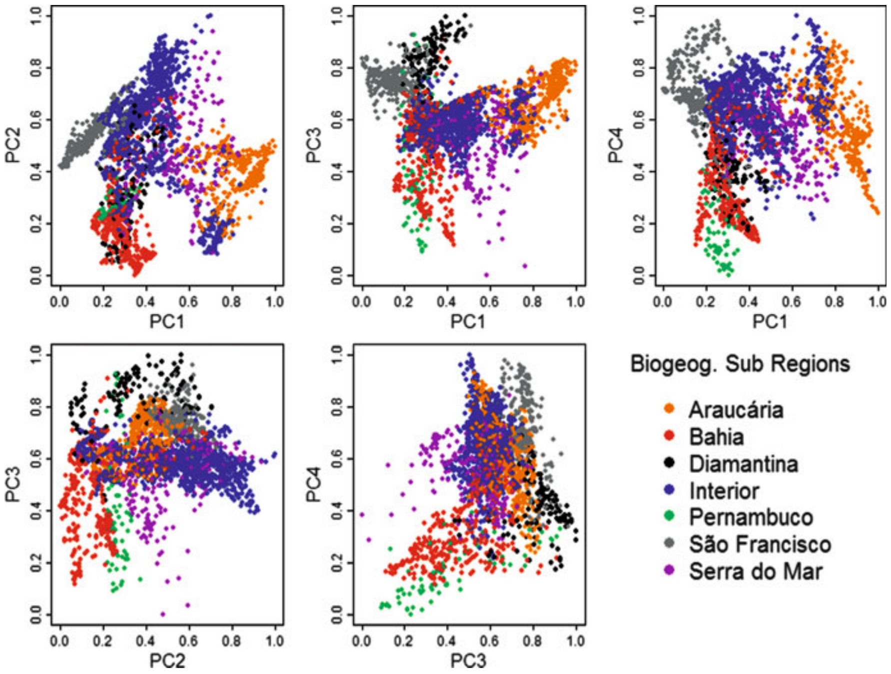

Fig. 21.2 Standardized principal components (PCs) for the first four axes obtained from the analysis of 19 layers from Worldclim 1.4 and an elevation map, of the Brazilian Atlantic Forest bioclimate environmental space. Each point ($n = 2{,}650$) represents a different sub-watershed of order 5a. Biogeographical subregions are identified by *colored dots*, not including the Brejos Nordestinos BSR given its size

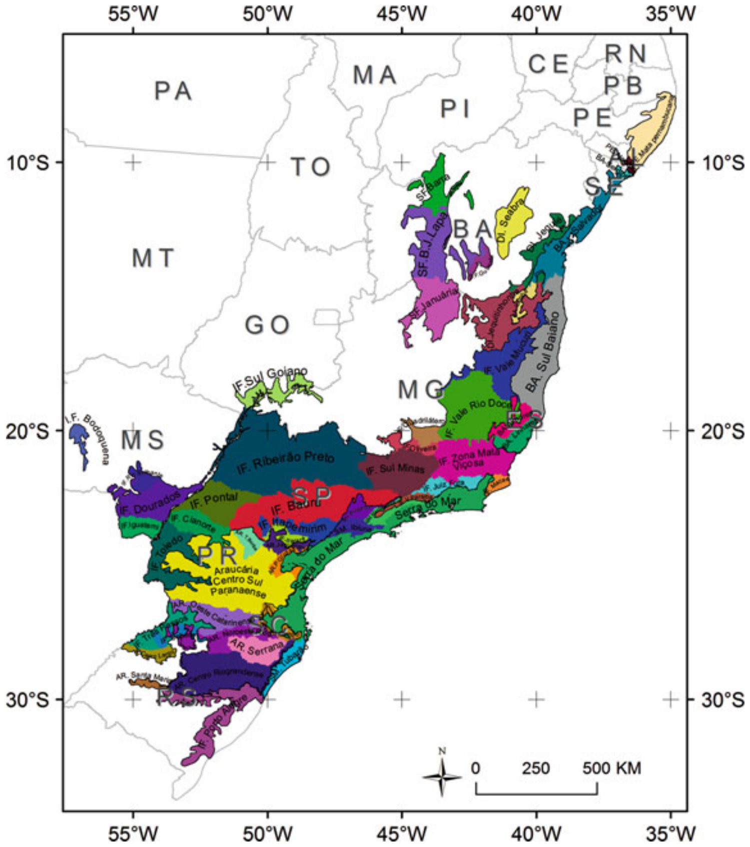

Fig. 21.3 Proposed subdivision of the Brazilian Atlantic Forest by biogeographical subregions [BSRs; Silva and Casteleti (2003), excluding the Brejos Nordestinos], considering clusters derived from 19 environmental layers (Worldclim 1.4) and an elevation map. The first two letters for new subdivisions identify the BSRs: *AR* Araucaria; *BA* Bahia; *DI* Diamantina; *IF* Interior Forest; *PE* Pernambuco; *SF* São Francisco; *SM* Serra do Mar

Table 21.1 Summary information for internal subdivisions proposed for the biogeographical sub-regions (BSRs; Silva and Casteleti 2003), excluding the Brejos Nordestinos, which were already too small

Biogeographical sub-region	Number of subdivisions	Area in ha			
		Minimum	Mean	SD	Maximum
Araucária	9	823,781	2,926,777	9,193,929	9,379,519
Bahia	6	200,941	2,223,135	2,197,306	5,575,259
Diamantina	3	1,645,058	3,598,382	1,691,630	4,577,447
Interior	25	50,713	2,848,668	3,309,680	14,805,211
Pernambuco	2	281,664	1,798,296	2,144,842	3,314,928
São Francisco	5	291,418	2,508,833	2,236,126	5,934,037
Serra do Mar	5	820,619	2,610,988	3,586,569	9,018,947

The subdivisions were generated based on bioclimate (14 environmental layers of Worldclim 1.4) and altitudinal variation data for the Brazilian Atlantic Forest

Most of the sub-divisions have less than 10% of forest remaining, thus below the target minimum percentage for biodiversity conservation (Secretariat of the Convention on Biological Diversity 2002). Type of forests, rain fall and temperature varied greatly between sub-divisions, from evergreen to deciduous forests, following an also extreme gradient of rain fall (varying between 800 and almost 2,000) and temperature (Table 21.2).

This new sub-division allows a better representation of the Atlantic Forest region considering the biogeographical data of Silva and Casteleti (2003), as well as information on bioclimatic and altitude. Field studies should now be conducted to understand the amount of biodiversity variation between subunits, to properly categorize the Atlantic Forest biota in order to support conservation and restoration plans.

21.3 Altitudinal Ranges and Geomorphometric Parameters Across the Atlantic Forest Distribution

Deforestation is recognized worldwide as a process that follows non-random patterns (Seabloom et al. 2002). Soil fertility, economic interests, proximity to urban settlements and roads are among the important factors that drive forest loss and fragmentation in tropical regions (Laurance et al. 2001; Gardner et al. 2009). In the Atlantic Forest, deforestation and regeneration processes are clearly influenced by altitude, topography, land use, and urban areas (Silva et al. 2007; Teixeira et al. 2009; Freitas et al. 2010).

21.3.1 Elevation Ranges

Recently, Tabarelli et al. (2010) quantified the original and present forest distribution across elevation ranges for the entire Atlantic Forest. Originally, more than 80% of the forest occurred at elevations from 200 to 1,200 m, and particularly between 400 and 800 m (Fig. 21.4). The original trends of the proportion of forest distribution between elevation ranges are still perceptible in the present remnants, but the percentage of forest remaining within each elevation range has changed dramatically (Fig. 21.4). Higher altitudes (>1,200 m) retain more than 20% of the original cover, reaching more than 40% for elevations above 1,600 m; whereas at altitudes from 400 to 800 m, only about 10% of the original forest still exists.

21.3.2 Relief Aspect Orientation

Aspect is a circular landform parameter that varies between 0 and 360° and indicates the flow line direction (Hengl and Evans 2009; Olaya 2009). This parameter is obtained from digital elevation models, and could be a good surrogate for

Table 21.2 Characterization of the proposed sub-divisions within each biogeographical subregion (BSR)

Biogeog. subregions[a]	Sub-divisions	Vegetation	Area (km^2)	Forest (%)	Elevation (m)		Precipitation (mm)		Temperature (°C)		Precipitation seasonality (%)
					Mean	SD	Mean	SD	Mean	SD	
Perna	PE-Mata pernambucana	Semidecidual forest/open forest	33,149	14.5	245	215	1384	363	23.5	1.3	60
Perna	PE-Alagoas	Semidecidual forest/Restinga	2,817	6.9	105	71	1107	202	24.6	0.5	66
Bahia	BA-Sul baiano	Evergreen forest	59,561	20.7	153	126	1209	198	23.9	0.6	32
Bahia	BA-Salvador	Evergreen forest	40,867	18.4	173	177	1466	336	23.7	1.3	36
Bahia	BA-Linhares	Evergreen forest	12,423	18.8	459	397	1223	91	22.0	2.3	52
Bahia	BA-Aimorés	Evergreen forest	11,020	9.2	375	276	1210	52	22.8	1.6	61
Bahia	BA-Itambé	Evergreen forest	7,459	10.2	638	202	864	94	21.5	1.3	48
Bahia	BA-Sergipe	Savanna/restinga	2,009	10.4	70	60	1101	182	25.2	0.4	63
S.Fran	SF-Bom Jesus da Lapa	Decidual forest	59,340	6.8	589	187	873	93	24.1	1.3	89
S.Fran	SF-Januária	Decidual forest	36,025	2.2	559	107	891	93	23.8	0.8	94
S.Fran	SF-Barra	Semidecidual forest/ecological transitional zones	20,904	3.2	526	133	855	101	24.6	0.9	87
S.Fran	SF-Guanabi	Decidual forest	9,172	9.6	852	272	783	121	21.6	1.6	81
Diam	DI-Seabra	Decidual forest/semidecidual forest	45,726	20.2	666	232	794	102	21.8	1.3	47
Diam	DI-Jequitinhonha	Decidual forest	45,590	12.6	659	252	857	78	21.9	1.3	71
Diam	DI-Jequié	Decidual forest	16,451	6.8	448	260	853	202	21.9	1.5	36
Inter	IF-Ribeirão Preto	Semidecidual forest/ecological transitional zones	145,235	4.9	540	196	1308	135	22.0	1.3	70
Inter	IF-Bauru	Semidecidual forest/ecological transitional zones	67,022	4.8	645	218	1327	132	20.2	1.3	59
Inter	IF-Vale do Rio Doce	Semidecidual forest	60,740	10.6	552	267	1268	141	21.8	1.7	78
Inter	IF-Zona da Mata/Viçosa	Semidecidual forest	42,484	9.9	530	331	1288	147	21.1	1.8	71
Inter	IF-Porto Alegre	Semidecidual forest	42,109	5.0	81	101	1425	104	18.8	0.7	12
Inter	IF-Vale Mururi	Semidecidual forest	41,885	12.9	519	248	1034	112	22.6	1.3	63
Inter	IF-Sul de Minas	Semidecidual forest	41,880	6.6	993	175	1525	103	19.2	1.2	75

(continued)

Table 21.2 (continued)

Biogeog. subregions[a]	Sub-divisions	Vegetation	Area (km^2)	Forest (%)	Elevation (m)		Precipitation (mm)		Temperature (°C)		Precipitation seasonality (%)
					Mean	SD	Mean	SD	Mean	SD	
Inter	IF-Dourados	Semidecidual forest	38,979	4.8	372	93	1471	100	22.8	0.5	39
Inter	IF-Toledo	Semidecidual forest	34,091	9.0	395	119	1643	156	20.1	1.0	24
Inter	IF-Pontal	Semidecidual forest	30,817	5.6	414	92	1259	73	21.6	0.9	43
Inter	IF-Sul goiano	Semidecidual forest	21,158	5.2	554	126	1392	112	24.0	0.9	78
Inter	IF-Cianorte	Semidecidual forest	18,865	4.9	413	114	1381	87	20.8	1.0	31
Inter	IF-Itapemirim	Ecological transition zones	18,187	7.1	634	88	1246	88	19.5	0.8	48
Inter	IF-Três Passos	Decidual forest	16,944	6.0	363	137	1844	76	19.8	0.6	10
Inter	IF-Juíz de Fora	Semidecidual forest	12,358	16.0	608	302	1440	109	20.4	1.6	72
Inter	IF-Iguatemi	Semidecidual forest	11,774	5.5	350	59	1569	47	21.9	0.2	30
Inter	IF-Cerro Largo	Decidual forest	10,814	3.0	294	108	1800	35	20.1	0.6	11
Inter	IF-Rio brilhante	Semidecidual forest/ecological transitional zones	10,455	5.0	345	42	1435	26	23.5	0.2	42
Inter	IF-Oliveira	Semidecidual forest	8,761	8.0	936	112	1444	58	20.0	0.7	82
Inter	IF-Quadrilátero	Semidecidual forest	8,027	17.1	955	156	1426	65	20.1	1.1	86
Inter	IF-Seberi	Decidual forest	6,908	8.1	433	139	1823	40	19.6	0.6	10
Inter	IF-Itararé	Ecological transition zones	6,358	4.9	671	132	1261	49	19.5	0.9	42
Inter	IF-Macaé	Semidecidual forest/restinga	5,404	8.2	20	44	1083	41	23.2	0.3	48
Inter	IF-Vale do Paraíba	Semidecidual forest	5,341	13.1	630	300	1467	162	19.8	1.7	70
Inter	IF-Bodoquena	Decidual forest	5,214	14.8	278	183	1276	45	24.4	1.1	52
S.Mar	SM-Contínuo da Serra Mar	Evergreen forest	88,594	45.5	418	378	1636	333	19.9	2.3	43
S.Mar	SM-Tubarão	Evergreen forest	12,850	20.0	143	198	1442	89	19.0	0.9	21
S.Mar	SM-Ibíuna	Evergreen forest	10,384	17.8	826	91	1622	347	17.5	0.7	54
S.Mar	SM-Bragança	Evergreen forest	8,910	9.1	941	252	1476	166	17.7	1.4	65
S.Mar	SM-Mantiqueira	Evergreen forest	8,206	14.1	776	270	1469	184	18.4	1.5	66
Arauc	AR-Araucária Centro Sul paranaense	Mixed forest	101,587	10.8	822	192	1632	179	17.5	1.2	23

Arauc	AR-Centro riograndense	Mixed forest/decidual forest	56,696	15.3	540	277	1656	182	17.7	1.3	14
Arauc	AR-Oeste catarinense	Mixed forest	23,747	10.3	841	219	1907	170	16.8	1.4	13
Arauc	AR-Noroeste riograndense	Mixed forest	22,511	5.7	702	177	1726	104	17.6	1.4	13
Arauc	AR-Serrana	Estepe savanna	17,672	15.1	1033	191	1651	76	15.5	1.0	13
Arauc	AR-Telemaco Borba	Mixed forest	8,475	8.3	790	114	1438	66	18.4	0.6	27
Arauc	AR-Jaguariaiva	Mixed forest	8,238	8.9	851	166	1339	80	18.1	1.2	39
Arauc	AR-Rio do Campo	Mixed forest	7,460	46.8	679	202	1554	79	17.2	1.0	21
Arauc	AR-Ponta Grossa	Mixed forest	7,167	23.5	825	160	1498	144	18.0	1.0	32
Arauc	AR-Santa Maria	Decidual forest	5,875	8.8	290	92	1760	30	18.9	0.4	7

BSRs are ordered from north to south, and sub-divisions within each of them, were ordered by their sizes. Predominant vegetation cover of each subdivision was obtained from vegetation map available from IBGE (2004). Elevation was obtained from SRTM DEM. Mean annual precipitation, mean annual temperature and precipitation seasonality were obtained from Worldclim database

[a] BSRs abbreviation: *Arauc* Araucária, *Bahia* Bahia, *Diam* Diamantina, *Inter* Interior Forest, *Perna* Pernambuco, *S.Mar* Serra do Mar, *S.Fran* São Francisco

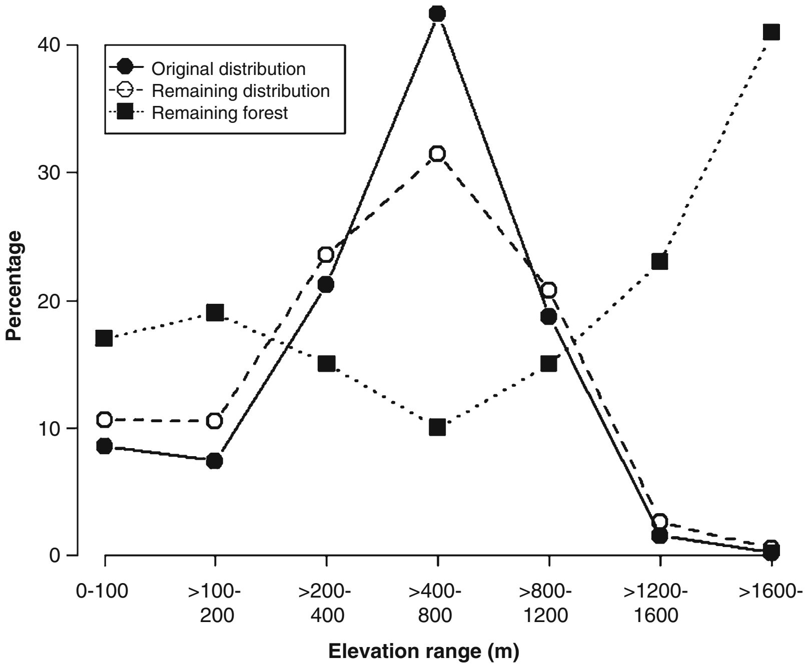

Fig. 21.4 The *circles* indicate the percentages of original and remaining Atlantic Forest distribution across elevation ranges. *Squares* indicate the percentage of remaining forest within each elevation range

solar energy irradiance, net primary production, biomass accumulation (Lu et al. 2002), species distribution (Kappelle et al. 1995), and land cover (Silva et al. 2008; Silva 2010). Since biodiversity is related to vegetation biomass and energy intake, understanding the spatial distribution of a forest in different terrain aspects can help to comprehend forest dynamics, as well as to support restoration programs. The Atlantic Forest relief is not equally distributed, and the aspect parameters vary widely along the biome. Here, we analyzed how the original and present Atlantic Forest remnants are distributed, when considering terrain aspect.

We extracted the terrain aspect parameter from the SRTM 1.4 data. We reclassified the original aspect data according to the eight cardinal directions, and quantified the amounts of original and present forest cover. We also combined this information with elevation data in order to understand how these two variables are influencing Atlantic Forest remains jointly.

The terrain aspect for the original Atlantic Forest distribution varied from 11 to 16% among the eight directions (Fig. 21.5a). No directional trend was observed for the original forest distribution (Rayleigh test, $t = 0.0076$; $p = 0.9445$), although it was slightly skewed towards west. In contrast, the remaining forest differs from the original one (Rayleigh test, $t = 0.5842$; $p = 0.000162$) by having

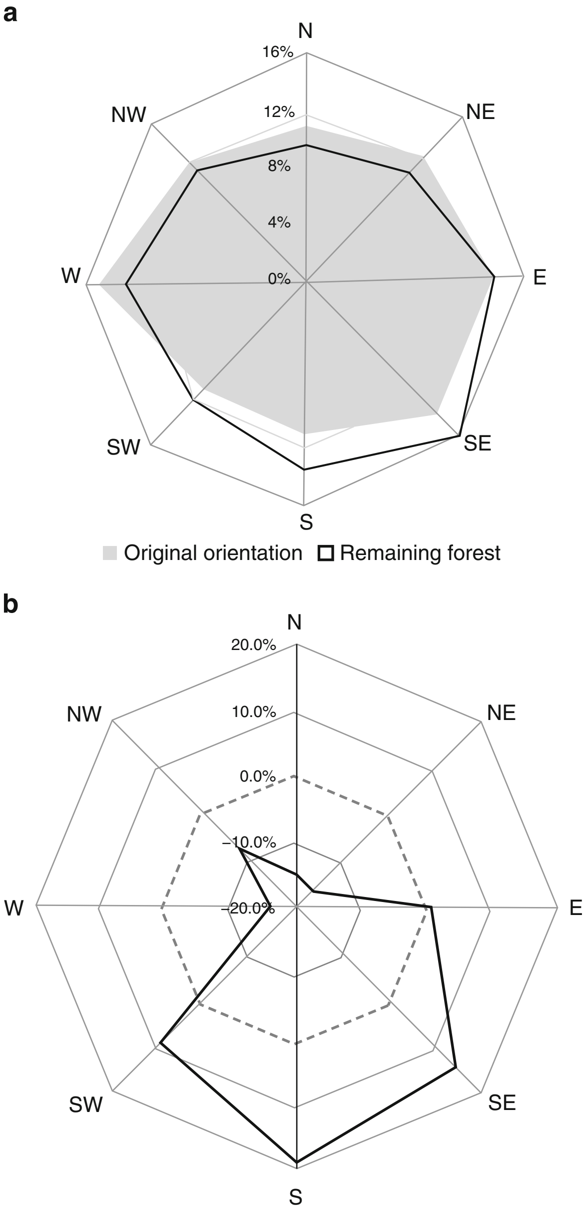

Fig. 21.5 (**a**) Aspect orientation in percentage for the original (*shaded gray*) and remaining (*solid line*) Brazilian Atlantic Forest (summing to 100%). (**b**) difference (in%; *solid line*) between the original and remaining forest distribution within aspect orientation, where positive values indicate less deforestation and negative values more deforestation in relation to the original distribution. *Dashed line* in (**b**) indicates zero difference between the original and remaining forest aspect orientation. Radar graph axis legend: *N* north; *NE* northeast; *E* east; *SE* southeast; *S* south; *SW* southwest; *W* west; *NW* northwest

20% more forests in the South compared to the average remaining Atlantic Forest. The Southeast and Southwest, respectively, show 14% and 9% more forests than on average in the entire Atlantic Forest, corroborating the pattern of more remaining forests southwards (Fig. 21.5b). These results are influenced by the Serra do Mar continuum (more than 1 million ha), which has a large fraction of its terrain facing

South and Southwest. However, and more important, these results reflect a land-use pattern that avoids the south-facing slopes (Mello 2009) due to the lower light intensity, which is less favorable for agricultural production (Silva et al. 2007). This leads to a higher amount of second growth forests given lower land use intensity in these areas.

Superimposing the present remaining forest, to the terrain aspect, and to the elevation zones, the South to Southwest orientations were the most represented for the two elevation ranges that include more forest (401–800 m and 801–1,600 m). In contrast, the elevation range of 0–100 m showed a slight tendency to include more forest in the West aspect direction. This elevation range is largely composed of coastal lowlands with mountains covering their west side that shade them in the evenings, particularly from the central part of the state of Rio de Janeiro toward the southern part of the Atlantic Forest. Other ranges of elevation did not show a predominant direction of terrain aspect.

21.4 The Remaining Forest and Its Spatial Distribution

The Atlantic Forest of eastern Brazil is essentially a complex mosaic of different ecosystems, each of them with a distinct species pool and patterns of human occupation, requiring different conservation and restoration efforts. This complexity and idiosyncrasies need to be clearly considered when conservation measures are to be taken, since precise actions will be extremely beneficial in terms of time and financial needs.

A shortcut to consider these particularities is to analyze the landscape structure, which has been widely used as a biodiversity surrogate in conservation planning (Williams et al. 2002; Lindenmayer et al. 2008), especially where inventory data and ecological information are not available (Fairbanks et al. 2001). Here, we review the available literature on the landscape structural patterns of Atlantic Forest remnants, particularly based on the findings of Ribeiro et al. (2009). We added new analyses and local examples to determine the importance of considering the fine scale in defining regional conservation and restoration planning (Ranta et al. 1998; Teixeira et al. 2009; Barreto et al. 2010). We mainly focused on describing the distribution of forest habitat patches, and did not include information about forest quality and degradation, which would demand a different approach.

21.4.1 Forest Amount

Although the overall amount of remaining Atlantic forest is around 12%, in some regions such as the São Francisco BSR and the Transition Forests the remaining habitat is very limited, as little as 4.7% in the case of the São Francisco (Table 21.3). In contrast, the Serra do Mar BSR has 36.5% of its original extent covered by

Table 21.3 Area of Atlantic Forest (ha and%) remaining in each biogeographical sub-region (BSR) according to Ribeiro et al. (2009)

	Remaining forest		Remaining restinga/mangrove		Total remaining Atlantic forest	
BSR	Area (ha)	%[a]	Area (ha)	%[a]	Area (ha)	%[a]
Araucaria	3,202,134	12.6			3,202,134	12.6
Bahia	2,047,228	16.7	115,059	0.9	2,162,287	17.7
Brejos Nordestinos	13,656	16.0			13,656	16.0
Diamantina	1,109,727	13.5			1,109,727	13.5
Interior	4,807,737	7.0	32,451		4,840,188	7.1
Pernambuco	360,455	11.5	19,363	0.6	379,818	12.1
Serra do Mar	3,678,534	32.2	491,263	4.3	4,169,797	36.5
São Francisco	499,866	4.7			499,866	4.7
TOTAL	15,719,337	11.26	658,135	0.47	16,377,472	11.73

[a] Percentages proportional to BSR area

forests, which makes it by far the best protected BSR. All other BSRs have 12–18% of forest cover (Table 21.3).

Overall, the percentage of forest within the fifth-order SWS is particularly low (Fig. 21.6). SWS with larger proportions of forest (>55%) been found along the coastal mountain ranges of the state of São Paulo, and particularly in the south-coastal region of São Paulo and the coastal region of Paraná. Outside the Serra do Mar BSR, only a few highly forested SWS occur on the south coast of Bahia, in the Iguaçu region in the Interior Forests, and also in the state of Rio de Janeiro (Fig. 21.6).

Landscapes with small amounts of forests (<15%) have been suggested to have biodiversity patterns that are more related to fragment size, since the overall connectivity is generally low to allow forest species to move among fragments (Martensen 2008). Therefore, we expect that in most of the SWS, fragment size would be a good surrogate for species diversity, and the larger patches should be a clear conservation priority. Regions with intermediate proportions of forests (~30%) have been shown to be highly influenced by connectivity patterns (Martensen et al. 2008; Dixo and Metzger 2009; Dixo et al. 2009). Such regions should therefore be targeted to increase connectivity, particularly between large remnants and the surrounding smaller forest fragments, and also to allow connectivity between larger blocks of forests, such as conservation units. Riparian forests, which are legally protected, are especially important and have proved to effectively protect riverine systems (Silvano et al. 2005; Roque et al. 2010), as well as terrestrial ones (Lees and Peres 2008).

21.4.2 Land Use Types

Since most of the Atlantic Forest is very close (<150 m) to forest edges, and thus to human modified ecosystems, land use has a very important influence in biodiversity conservation. Sugarcane, for instance, was the first crop to be planted extensively

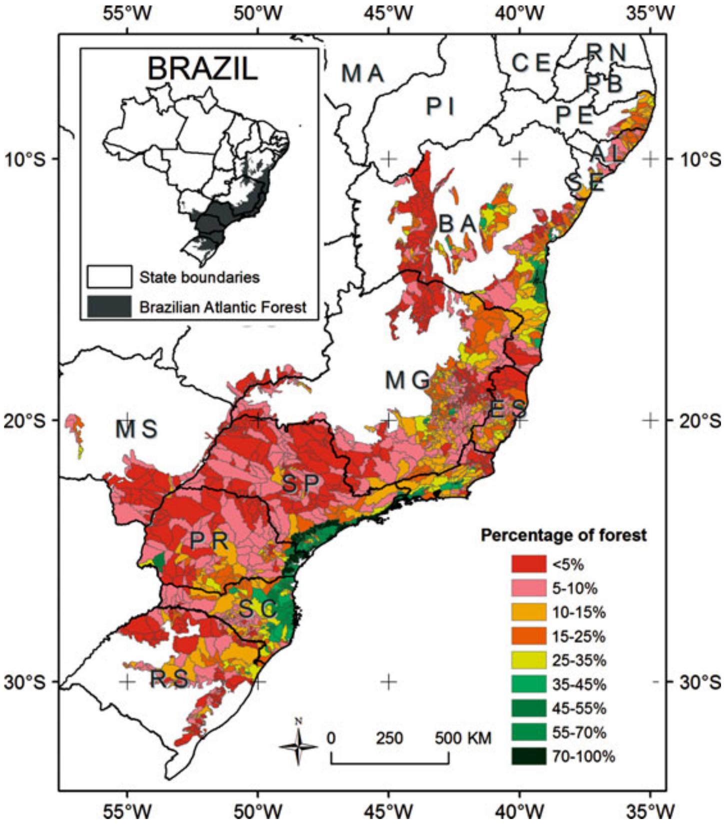

Fig. 21.6 Percentage of remaining Brazilian Atlantic Forest within the 2,650 sub-watersheds of order 5a, as proposed by Pfastetter (1987)

in the Atlantic Forest, beginning early in the sixteenth century and starting an intensive forest conversion process. Later, coffee plantations in the states of Rio de Janeiro, São Paulo, and Paraná pushed the logging frontier forward. Today, sugarcane, pastures, *Eucalyptus* and Pine plantations share the landscapes that were formerly covered by the rich Atlantic Forest. Farm sizes vary according to the region, and are usually larger in favorable sites for modern agriculture. Oliveira Filho and Metzger (2006) observed that for Amazonian regions, large properties, usually present larger and more isolated fragments, when compared to smaller ones, which present fragments of smaller size and more connected by corridors or by close proximity to others, a pattern which is usually corroborated elsewhere. Since the early economic cycles in Brazil, the general agricultural pattern has been based on large monoculture properties and even today, this pervasive system continues, with high land concentration, since 15% of the properties cover more than 75% of the country's farmland (IBGE 2006). Large landowners usually occupy the best farmland, flat or gently sloping (<15%), leaving the steep hills for the small farming families. Small farms comprise more than 84% of the properties, but cover only around 24% of the agricultural land (IBGE 2006). Although occupying less than one-fourth of Brazilian farmland, small family properties are responsible for around 80% of the country's food base, sustaining the country food sovereignty (IBGE 2006). However, in flat areas where mechanization is possible, sugarcane plantations have taken over the land for biofuel (Lapola et al. 2010), which should actually be termed agrofuel (Altieri 2009a, b), also accompanied by soybeans and other large scale crops, including outsized pasture lands.

Following this general deforestation pattern, different types of matrix (i.e., non-forest; Gascon et al. 1999) were established in the Atlantic Forest region (Ribeiro et al. 2009 suppl. material). Cattle ranching and agriculture are the two predominant matrices found in the biome, and particularly cover a large part of the Interior Forest sub-region. In the Araucaria and southern Bahia sub-regions, forestry plantations (*Pinus* and *Eucalyptus*; Fonseca et al. 2009; see also Ribeiro et al. 2009 suppl. material) are among the most important types of matrix, although agriculture and ranching are predominant. The state of São Paulo is particularly covered by sugarcane plantations, which still expanding (Rudorff and Sugawara 2007; Nassar et al. 2008), pastures (Brannstrom 2001; Durigan et al. 2007), and a growing number of *Eucalyptus* plantations. The Pernambuco sub-region is also dominated by pastures and agriculture fields, with dominance of sugarcane plantations (Trindade et al. 2008; Kimmel et al. 2010; Silva 2010).

Traditional sugarcane harvesting is based on burning the crop, which causes problems of air pollution and also accidental spread of fire into the surrounding forest fragments (Durigan et al. 2007). The mechanization of sugarcane harvesting, while diminishing previous impacts, including the reduction of inhumane working conditions (which caused deaths and severe health problems, Silva 2008), has also caused a reduction in the connectivity between forest fragments, since isolated trees have been cut down to facilitate mechanical harvest. Isolated trees considerably increase the connectivity between fragments (Harvey et al. 2004), and thus their loss should be properly compensated by additional connectivity features such as corridors, which can compensate the homogenization caused by sugarcane plantations, especially in the state of São Paulo. Similar recommendations for conservation can be made elsewhere, especially when forest fragments are already interspersed among the plantations or pastures.

Recently, vast *Eucalyptus* plantations are gaining ground, based on huge well-capitalized corporations from other economical fields that possess the financial power to acquire vast landholdings. These corporations have focused on acquiring the cheap small hilly properties, as forestry technologies evolve to operate on steeper terrains. This process has contributed to urban growth through intensifying migration to urban areas. Forestry has proved to be the "beauty" in some cases where good ecological management practices are employed (Fonseca et al. 2009). In other cases, unfortunately more common nowadays, is proved to be "beast," where management is only focused on high productivity not always sustainable in social and environmental aspects (Zurita et al. 2006). Large plantations of a few clones, short cycle rotation, understory cleaning, and intense chemicals use are among the most common practices employed in modern forestry, which are detrimental to environmental conservation.

Another large fraction of the farmland in the Atlantic Forest is covered by pastures. Most of them are lightly managed, and still containing scattered trees that sometimes form small forest patches in different early successional stages. Intense debate is occurring about the conversion of these areas into intensively managed fields, especially sugar cane, with claims that this will allow higher production and economic gains. Besides, the clear positive financial advantages of these proposals, negative aspects such as decreasing matrix permeability, increasing dependency on non-renewable resources, and increasing the use of chemical products, as well as the far-reaching social impacts of these agricultural practices will occur in the Atlantic Forest region, while the benefits will be felt mostly elsewhere, such as lowering habitat conversion in the Cerrado and Amazon, since habitat conversion in the Atlantic Forest is already low. From another side, in order to access water, cattle cause large impacts in riparian forests and riverine systems, which could reduce their potential to promote corridor connections between fragments. Moreover, fire is also commonly employed as a management technique in pastures, which, in combination with cattle occurrence in the surrounding fragments, results in the degradation of nearby forests.

21.4.3 Number of Forest Fragments and Their Size

The Atlantic Forest is patchily distributed in 245,173 forest fragments of varying size. Although some large fragments still exist, such as those that extend along the coastal mountains of southeast Brazil, especially in the states of São Paulo, Paraná, and Santa Catarina, most of the forest fragments (83.4%) consist of patches smaller than 50 ha, which is expected to severely compromise biodiversity conservation (Lindenmayer et al. 2006; Laurance et al. 2007). Only 77 fragments (0.03% of the total fragments) are larger than 10,000 ha, which highlights the very poor conservation condition of the unique Atlantic Forest biota.

In all BSRs, small fragments (<50 ha) were by far the most numerous ones. The most distinct pattern occurs in the Serra do Mar region, which in addition of having the largest fraction of fragments smaller than 50 ha, similarly to the other regions, has more than half of its forests in large fragments (>50,000 ha). Moreover, this region is the only one that contains a forest fragment larger than 1 million ha, and also contains the second and third largest fragments of the entire remaining Atlantic Forest. In all other regions, the largest fragments are <250,000 ha, and only the Araucaria Forest ($n = 4$) and the Interior Forest ($n = 1$) also contain fragments >50,000 ha, respectively, the inland forests of Santa Catarina, including the São Joaquim National Park, and the Iguaçú National Park in Paraná. In the Bahia BSR, the largest patch has approximately 29,000 ha, while in the São Francisco and Pernambuco none exceeds 10,000 ha, and in Diamantina none is larger than 25,000 ha.

21.4.4 Forest Core and Edge Area

Landuse patterns in the Atlantic Forest region have generated intensive fragmentation, resulting in an impressive amount of forest edges. Today at least 73% of the remaining forest is located less than 250 m from any forest edge and 46% is less than 100 m apart from any edge. Only 7.7% is located farther than 1,000 m, and around 12 km is the longest distance that one can penetrate into the forest from any edge. The pattern is similar for every BSR, again with the exception of the Serra do Mar. Whereas all BSRs have edge forests (100 m from edges) in amounts of at least 40% to as high as 60% in Pernambuco, Serra do Mar has only 25% of its remaining forest less than 100 m from forest edges. This relatively small edge effect is reflected in the higher proportion of core areas, i.e., more than 256,000 ha farther than 2.5 km and almost 57,000 ha farther than 5 km from edges. The largest block in the Atlantic Forest is located in the Serra de Paranapiacaba, in the state of São Paulo, Serra do Mar BSR, which together with the Iguaçú National Park in the Interior BSR are the only two fragments that have forests deeper than 12 km from any edge.

21.4.5 Connectivity Patterns

The capacity of a species to cross open areas is directly associated with its potential to maintain sustainable populations in the present fragmented conditions of the Atlantic Forest. Species that are not able to cross open areas, i.e., obligate forest species, have a functionally connected mean area of only 64 ha, while a species that is capable of crossing 50 m have a mean functional area of around 200 ha. The largest functionally connected cluster for species capable of crossing 100 m comprises the largest fragment of the Serra do Mar and the nearby fragments. All together, this cluster totalizes more than 2.8 million ha (18% of the total remaining forest), and stretches from the state of Rio de Janeiro all the way south to Rio Grande do Sul, comprising the largest "corridor" of the Atlantic Forest. In the Bahia region, species that can cross short gaps such as 100 m can reach a functional area of 50,000 ha (17% of the remaining forest in the region). In the other BSRs, the distances to reach a functionally connected area of this size are always large, up to 400 m in the São Francisco and more than 500 m in the Pernambuco BSRs.

The mean distance between fragments in the entire Atlantic Forest is around 1,441 m, but it varies widely. The importance of the small fragments in reducing isolation is enormous. For example, when fragments <50 ha are excluded, the mean isolation increases to 3,532 m, and when fragments smaller than 200 ha are excluded, the mean isolation reaches more than 8,000 m, which highlights the immense importance of these fragments in sustaining viable populations in the region. This is vital in all regions, but it is particularly important in the São Francisco and in the Interior Forest, although of less importance in the Serra do Mar, since most of the remains are clumped in one or a few large fragments.

21.4.6 The Role of Nature Reserves in Protecting Atlantic Forest Biodiversity

Brazil and South America have the world's largest proportion of land in protected areas (Brockington et al. 2008). However, this proportion increased in the last two decades, when the Atlantic Forest biome had already been turned into a myriad of fragments of varying sizes, and thus, beneficiated mainly the Amazonian region. Therefore, the today's total protected area of the Atlantic Forest is approximately 2.26 million ha, which represents only 1.05% of forests of the original cover distribution, way below the 10% recommended by the Global Strategy for Conservation (Secretariat of the Convention on Biological Diversity 2002; Rodrigues et al. 2004). Nature reserves protect 9.3% of the Atlantic Forest remnants, however, differently according to the regions. The Serra do Mar BSR, for example, which is by far the best protected one, has approximately 25% of its remaining forests under some type of restriction. This represents only 8.11% of its original cover, stills lower than the 10% target (Secretariat of the Convention on Biological Diversity 2002). All other BSRs present lower amounts of remaining forest preserved, such as the Interior Forests (6.8%) and Bahia (4.2%), and all others have even less than 4%. Today, restrictive legislation protects all the Atlantic Forest remnants (Lei da Mata Atlântica); however, law enforcement is negligent even in some of the Conservation Units.

Some reserves are contiguous, and thus we could identify seven large protected regions with areas around 100,000 ha. Five of them are in the Serra do Mar region: (1) Serra do Mar State Park, SP and Bocaina National Park, SP/RJ; (2) the former Jacupiranga State Park, SP, which today is a mosaic of Integral Protection and Sustainable Development units, and Superagui National Park, PR; (3) the Paranapiacaba continuum, composed of the PETAR State Park, Intervales State Park, Xituê Ecological Station, and Carlos Botelho State Park, all in the state of São Paulo; (4) the Serra do Tabuleiro State Park, SC; and (5) the Juréia mosaic, composed of the Banhados de Iguape Ecological Station, Juréia-Itatins Ecological Station, Itinguçu State Park, and Prelado State Park (SP). Recently, this last region has been the focus of intense debate between stakeholders, local communities, conservationists, and people involved in urban development, and the limits of the conservation units might be modified in the near future, to accommodate different interests in the region. The two other regions of large blocks of Nature Reserves are in the Interior Forest, the Iguaçú National Park (PR), the most important remnant of the interior forests; and in the Diamantina region, where the Chapada Diamantina National Park encompasses a considerable mosaic of open habitats, more related to the Cerrado biome, and some forest blocks. Together these large blocks of Nature Reserves encompass 1,212,800 ha, which comprises 53.6% of all protected areas. Moreover, 17 reserves range in size from 20,000 to 60,000 ha, also a considerable size in the today's scenario, and represent an additional 26% of the total forest under protection; these reserves are particularly located in the Interior, Serra do

Mar, Bahia, and Araucaria centers. The remaining forest under protection (~20%) is scattered in small reserves in all the Atlantic Forest regions.

Of the remaining forest outside the conservation units, only 22.6% is located within 10 km of any nature reserve, whereas 61% is farther than 25 km. The patterns within the biogeographical regions are similar, again with the Serra do Mar as the sole exception, where almost 60% of the remaining forest is less than 10 km from conservation units, which provides these forest fragments with some connectivity to large blocks of preserved forests.

21.5 Conservation of Marginal Habitats

It has been shown that for conservation purposes, the Atlantic Forest should be treated as a whole; including both rainforest and non-rainforest covers (Scarano 2002, 2009). Marginal habitats are extensions of the core rainforest and also serve as a buffer zone for it, because of the intimate floristic relationships that they maintain and also the animal transit between them, despite marked fragmentation. Since landscape history affects the present distribution pattern of species in fragmented landscapes, this history should be considered in conservation planning (Metzger et al. 2009). Interestingly, as seen in the above data, there is also a strong bias in the distribution of conservation units between forest and non-forest habitats of the Atlantic Forest biome. Rocky outcrops, above the tree line or on inselbergs, are mostly well protected and maintain a fauna and flora that is often relict and highly endemic, but has many close relatives within the neighboring rainforest. Lowlands, conversely, are poorly protected. Restinga vegetation is often replaced by housing and touristic complexes, because of the obvious attractiveness of the Brazilian coast. Swamp forests have been widely affected by drainage, either due to replacement by agriculture or efforts to eradicate tropical diseases in the early twentieth century. The fact that these types of habitats have lower species richness and lower rates of endemism than thus the core rainforest does not help either, and makes them less of a priority, particularly when the conservation currency is merely quantitative, counting the number of species and the number of endemics, and not considering genetic particularities present in this areas. Restingas and swamps are geologically younger, and most species found in these areas are from the rainforest. However, the stressful nature of these habitats has promoted the expression of plastic types of the original rainforest species, which are living evidence of what is perhaps the rainforest's main treasure: its genetic diversity (Scarano 2009).

A sad example of the failure of the legal system to treat the Atlantic rainforest as a whole, i.e., to include non-rainforest vegetation types, has been reported by Sá (2006). The peculiar coastal dry forest found in Búzios municipality in the state of Rio de Janeiro is a relictual vegetation that much resembles physiognomically the *caatinga* vegetation found in the semiarid region of the Brazilian northeast. Previous efforts to classify Brazilian vegetation types have labeled Buzios dry forest as a *caatinga* vegetation type, thus not protecting this highly touristic attractive regiont under the "*Lei da Mata Atlântica*," since it was classified as caatinga. However, Sá (2006) has shown that the floristic similarity between the dry forest and the Atlantic Forest is over 80%.

We make three recommendations for a conservation strategy that is more inclusive of marginal habitats (1) laws must be enforced and government must lead in providing good examples. Brazil has a sad record of not compensating landowners when their lands are seized for protected areas; (2) private protected areas have a successful history in the Atlantic Forest biome, and should be further supported; (3) the design of future protected areas and of future restoration initiatives should aim to promote connectivity not only along the forest–forest axis, but also along the forest-sea axis.

21.6 Ecosystem Services and Forest Restoration

Beyond the conservation of species richness and endemism, the interactions among species and between species and the abiotic environment support, regulate, and provide the services and cultural benefits that people derive from biodiversity (Benayas et al. 2009; McNeely et al. 2009). For instance, although not much is left of the Atlantic Forest biome, the existing remnants safeguard freshwater, climate, and food production, among other securities. The water available for the nearly 50% of the Brazilian population that lives in coastal regions, including large cities such as Rio de Janeiro and São Paulo, either springs from or is bordered by Atlantic Forest. The emerging carbon market indicates that these remnant forests not only ameliorate local climate in an otherwise fully urban landscape, but might also contribute significantly to the global carbon balance. Pollination, pest control, and erosion regulation are all provided by natural remnants of the Atlantic Forest. Furthermore, most of the cities are surrounded by forest fragments, and people use these natural areas for recreation.

Of course, reduced and fragmented as it is now, the provisioning of all such essential services for human well-being is under serious threat. Most of the Atlantic Forest is less than 200 m from any forest edge (Ribeiro et al. 2009), and therefore 200 m from a land-use area. More than 100 million people live in the region formerly covered by Atlantic Forests, in both rural and urban areas, including more than 3,000 cities and extensive agricultural fields and grazing land. Moreover, most of the remaining Atlantic Forest was already clear-cut or severely altered by humans, some parts even before European colonization. Finally, almost all of the remaining forests are located on private land; some of them have people living there or somehow related to the area. All of these reasons make it imperative to consider the human perspective in any conservation plan for the Atlantic Forest region.

Recently, Ribeiro et al. (2009) exposed the precariousness of the Conservation Unit System in the Atlantic Forest, which protects around 1% of the original vegetation. The need to expand this system is obvious. However, the efficiency of the existing units is already questionable, since most of them have problems in reaching their conservation targets. The several reasons for this include problems with unit protection and management, and also with the relationships with the surrounding human communities. Moreover, indigenous peoples have been moving to Conservation Units (Cardoso Island State Park and Intervales State Park in the state of São Paulo are two examples), since they are the only places remaining where they can maintain at least some of their original culture, and that are not private lands. This development has posed a challenge to conservationists, to modify their ways to deal with traditional peoples inside conservation units, since both groups have similar goals.

Presently, more than 90% of the remaining forests, including almost all the deforested areas, are located on private land. Therefore, conservation management must be adapted to these conditions. Forest restoration has been suggested as one of the key actions to be implemented in order to achieve Atlantic Forest conservation (Ribeiro et al. 2009; Rodrigues et al. 2009). However, effective means to engage people in landscape management and forest restoration are still lacking (Rodrigues et al. 2009). The estimated amount of forest that must be restored merely to comply with current Brazilian environmental legislation and also to restore agricultural areas that are not prone for adequate land use management (like degraded pastures in steep relief) is immense, and 15 million ha is expected to be restored up to 2050 (http://www.pactomataatlantica.org.br). Except for a few large (hundreds of hectares) restoration projects (see examples and different experiences in Rodrigues et al. 2009), most of the experiments are small and locally focused, and have not published their results and/or properly monitored their programs. This lack of information makes it more difficult to reach appropriate conclusions to help with future restoration actions (Rodrigues et al. 2009). An important rural economy could be enhanced by a massive restoration program in the Brazilian Atlantic Forest, since seed collection (see example in Instituto Refloresta, formerly Ecoar Florestal, www.refloresta.org.br), sapling production in community nurseries, and restoration implementation and maintenance could be conducted by small local farmers as a source of supplementary income. We also suggest that our biogeographical subdivision could be used as an initial surrogate to define regions to collect seeds for restoration projects, since local adaptations could have arisen from local selective pressures for different species.

Large landowners who produce agricultural commodities that are largely exported to Europe and North America as well as used in the local economy, should be obligated to comply with the environmental regulations, including taxation and moratoriums on products that excessively impact the environment. The Amazon Soy Moratorium appears to have had some relative success, and could be even more efficient in regions where the land-use patterns are better established. Small landowners should receive governmental incentives to environmentally improve their properties, including payment for environmental services, abundant technical and financial support for forest restoration, and relaxation of the laws regulating agroecological activities in key areas not yet covered by forests, particularly focusing forest restoration. Areas along the rivers are a main priority, since they can link fragments, allowing populations to maintain themselves in functionally connected fragments (Martensen et al. 2008); as well as protect river systems (Silva 2003).

21.7 Agroecology: Opportunities for Atlantic Forest Conservation

Agroecology, now at the fore of the conservation debate, has proved to enhance food production, biodiversity conservation, and poverty alleviation (Jose 2009). Tropical countries in general are particularly favorable for agroecological production, because of particular social and environmental aspects. Steeper and higher areas usually have larger amounts of forest (see above), and are usually occupied by family raised farms. These areas should be the focus of governmental efforts to make production in agroecological systems viable. The possibility of realizing profits from the multiple gains of this type of system should be explored. For example, ecosystem services such as those related to the maintenance of water quality and quantity, minimization of erosion, and biodiversity conservation (reviewed in Jose 2009 and Benayas et al. 2009) must be evaluated. Also, some effort must be made to aggregate better values to forest products, which are largely free of chemicals and could be produced with low impact. In some cases, restoration methods should be conceived in order to allow economic outputs for farmers, especially in the initial stages of succession, when diminishing costs is imperative to reach the large scale restoration needs in the Atlantic Forest. Moreover, restored forests could be manage to generate incomes out of timber and specially non timber products, including fruits, honey, medicines, seeds, and others. Timber production in diversified plantations of native trees should act as a permeable matrix for forest species, in the same time that reduces the demand of the mostly illegally harvest Amazonian wood.

Changing the common concept of forests as unproductive areas is imperative to protect Atlantic Forest biodiversity. There are many examples of agroforest systems in every region, which stand out as highly productive systems with low environmental impact. Among the better known are the “cabrucas” on the south coast of Bahia (Alvim and Nair 1986; Schroth and Harvey 2007), where shade cocoa is planted and the environmental benefits over other production systems have been largely explored (Pardini et al. 2009). In the Ribeira Valley located in the Serra do Mar BSR in São Paulo (REBRAFE 2007), there are also some very good examples of highly diverse and productive systems, which produce many agricultural goods and fruits, as well as forest products. Examples in the Interior Forests are also abundant, such as in the Pontal do Paranapanema (Cullen et al. 2004). In the Araucaria subregion, systems that mix trees, such as the *Araucaria angustifolia*, and pastures, locally called “faxinais,” are widespread. Also in southern Brazil there are some examples that combine timber trees, perennial cash crops, and the South American holly (*Ilex paraguariensis*) (REBRAFE 2007). Some experiments have been indicating a good potential to the use of agroforests as elements to improve connectivity between fragments (Cullen et al. 2004; Uezu et al. 2008; Pardini et al. 2009), to decrease edge effects by functioning as buffer zones (Cullen and Fenimore 2002; Cullen et al. 2004), to reduce soil erosion (Franco et al. 2002), to increase soil fauna (REBRAFE 2007) and biodiversity in general (Schroth et al. 2004; McNeely and Schroth 2006; Jose 2009), and also to increase soil fertility (REBRAFE 2007). Vieira et al. (2009) emphasized the contribution of agroecology techniques as a transition phase that stimulates early forest restoration with a so called "agrosuccessional" restoration strategy, which has been used as a way to induce landowners to restore forests. The social aspects of agroforest systems in the Atlantic Forest are also normally evaluated, and enormous benefits have been reported (Franzen and Mulder 2007; Vieira et al. 2009).

21.8 Conclusions

The Atlantic Forest region is one of the top world's hotspot for biodiversity conservation, and should be a global target for conservation. In this chapter, we explored the characteristics of the biota and the forest distribution, pointing out some weaknesses in its conservation. Most importantly, we presented clear objectives to be aid in its conservation agenda.

A great cause of concern is the rapid expansion of large monocultures, particularly sugarcane and *Eucalyptus* plantations, which could threaten the last forest remnants, in particular by decreasing connectivity between them and causing additional edge effects, especially in the case of agricultural land uses. Moreover, the expansion of these systems had intensified migration of people from rural to urban areas, which has had additional environmental impacts on urban areas.

One key point is that Atlantic Forest conservation is impossible without a clear consideration of the human role, since most of the remaining forest is located on private lands. An effective Atlantic Forest conservation plan should start with making the approximately 110 million people now living in the region aware of its global importance and its present fragile situation. Such a plan should target the preservation of the last large remnants, but should also incorporate agricultural land, within a fragmented landscape management perspective. Small family farms are usually located in steeper areas where forest remnants are usually more abundant, and where low impact agricultural production could be both socially and environmentally beneficial. Restoration should be a clear target, and an immense reforestation effort should be made, focusing on creating clusters of fragments that are functionally connected, particularly by riparian corridors, which can produce multiple benefits. Payment for ecosystem services should be rapidly implemented in certain key conservation regions, which will probably foster conservation on small properties.

Despite the unsatisfactory present state of conservation, the Atlantic Forest still harbors a huge amount of biodiversity, including many endemic species. Urgent conservation actions should be taken focusing on clear targets, in order to promptly implement management plans and avoid massive loss of biodiversity. Some steps are presented here, and we urge that they be taken sooner rather than later.

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Chapter 22
Sustainable Development and Conservation of Biodiversity Hotspots in Latin America: The Case of Ecuador

Marco Rieckmann, Maik Adomßent, Werner Härdtle, and Patricia Aguirre

Abstract The conservation of biodiversity is closely linked to sustainable development. This is particularly evident in the so-called developing countries. Latin America, for instance, hosts some of the most important biodiversity hotspots in the world. However, this biodiversity is threatened by development processes which lead to environmental degradation and thus a significant loss of biodiversity. In Ecuador, new approaches towards sustainable development with a particular focus on biodiversity conservation and environmental protection have been developed in recent years. Against the background of data on biological diversity in Latin America and a description of conservation endeavours in the Latin-American region, this chapter analyses the Ecuadorian efforts to achieve sustainable development and long-term protection of biological diversity. Positive impacts as well as new challenges and conflicts, which result from these approaches, are identified and discussed.

22.1 Introduction

Efforts to conserve biological diversity are only as sustainable as the social and political context within which they take place (Hanson et al. 2009). This is particularly evident in the so-called developing countries.

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For instance, the Latin-American region is characterised on the one hand by a high level of biodiversity and on the other by the existence of manifold socio-economic problems. Policies and economic activities that strive towards socio-economic development and welfare often result in environmental problems and biodiversity loss (cf. Larrea 2009). Consequently, the question is how the conflict between economic progress and biodiversity conservation can be reconciled.

In recent years, both the Ecuadorian government and the civil society have developed new approaches for sustainable development that focus particularly on biodiversity conservation and environmental protection. Rights of nature and the concept of "Sumak Kawsay" ("Good Living") were incorporated into the new Ecuadorian constitution adopted in 2008. The Yasuní-ITT initiative commits Ecuador to leaving underground 20% of the country's total oil reserves, located in the ITT oil fields, within the Yasuní National Park. Hence, Ecuador is taking the initial steps towards moving from an oil-based economy to a new sustainable development model.

This study describes and analyses the current governmental and non-governmental programmes in Ecuador that are geared towards sustainable development and a long-term protection of biological diversity. Against the background of data on biodiversity in Latin America and a description of conservation endeavours in the Latin-American region, this paper identifies and discusses both the positive impacts and the new challenges and conflicts resulting from these approaches.

22.2 Biological Diversity of Latin America

There is evidence that Latin America hosts some of the most important biodiversity hotspots in the world, namely the Tropical Andes, Chocó/Darién/Western Ecuador, Central Chile, Brazil's Cerrado, and Brazil's Atlantic Forest (Harcourt 1999; Myers et al. 2000). Among these, the Tropical Andes and Brazil's Atlantic Forest are considered as "leading hotspots", since they are characterised by an extraordinary biological diversity when compared with other hotspots worldwide (Myers et al. 2000). The Tropical Andes, for example, are believed to harbour about 45,000 plant species (corresponding to 6.7% of global plants) and about 3,400 vertebrate species (corresponding to 5.7% of global vertebrates; Table 22.1). With more than 1,660 bird species (which corresponds to about 16.8% of the world's avifauna), the Tropical Andes proved to be the most important avifauna hotspot in the world (Table 22.1). This means, in turn, that many Latin-American countries (such as Colombia, Brazil, Ecuador, Peru, and Chile) are characterised by an extraordinary diversity with regard to several taxonomic groups. Brazil, for example, is considered to host the earth's richest flora, at least 50,000 species or one-sixth of the planetary total. However, Ecuador with its mega-diverse flora comprising more than 25,000 plant species (and thus twice the number of plant species found in Europe) is no less diverse when the species richness of this country is related to its size (Kreft et al. 2004; Vargas Meza 2002). Regarding vertebrates, for example, Ecuador has the

Table 22.1 Species richness (of different taxonomic groups) for biodiversity hotspots in Latin America and Ecuador (according to Myers et al. 2000; Vargas Meza 2002)

Hotspot	Plant species	Endemic plants	Vertebrate species	Endemic vertebrates	Bird species		Mammal species		Reptile species		Amphibian species	
					Total	Endemic	Total	Endemic	Total	Endemic	Total	Endemic
Tropical Andes	45,000	20,000	3,389	1,567	1,666	677	414	68	479	218	830	604
Chocó/Darién/ Western Ecuador	9,000	2,250	1,625	418	830	85	235	60	210	63	350	210
Central Chile	3,429	1,605	335	61	198	4	56	9	55	34	26	14
Brazil's Cerrado	10,000	4,400	1,268	117	837	29	161	19	120	24	150	45
Brazil's Atlantic Forest	20,000	8,000	1,361	567	620	181	261	73	200	60	280	253
Ecuador	25,560	5,348	2,794	436	1,616	52	362	30	394	114	422	240

highest species density worldwide (i.e. the number of species per area; 2,794 in total, corresponding to 12% of the global vertebrate species richness; Table 22.1).

Several factors, such as variations in geological and edaphic conditions and the high environmental diversity in terms of extreme differences in altitude, precipitation, and annual mean temperature, are responsible for the extraordinary biodiversity found in Latin America (Sarkar et al. 2009). Patterns of broad-scale plant species richness, for example, are thought to be largely determined by (1) variation in insolation and water availability between different areas (species energy hypothesis), (2) habitat and topographic heterogeneity (spatial heterogeneity hypothesis), and (3) regional differences in geographic configuration and history (regional effects hypothesis; Distler et al. 2009). Geospatial and environmental data have been used in correlative models to identify conservation priorities on a landscape or a regional scale (in South America for example by Peralvo et al. 2007).

Because of its high species richness and endemism, Latin America in general, and biodiversity hotspots such as the Chocó and the Tropical Andes, in particular, have been a major focus of biodiversity conservation interests in recent decades (Sarkar et al. 2009). However, despite increasing conservation efforts, the biological diversity of Latin America is under continued threat from a variety of factors, including an accelerating rate of forest clearing, due to logging, and the resulting increase of arable area (Ojeda et al. 2003). In Central America and northern parts of South America, deforestation rates amounted to about 1% year^{-1} from 2000 to 2005, and human population growth rates were over 2% year^{-1} (FAO 2005). Bryant et al. (1997) estimated that about 30% of the region's primary and secondary vegetation has been completely transformed into agricultural fields and urban settlements. This development constitutes an increasing problem for both the protection of Latin America's biodiversity and human welfare, since the majority of the human population in many regions of Latin America relies on biological resources taken directly from the wild. Consequently, in Latin America, the extent and importance of nature conservation has increased significantly in the last few decades.

22.3 Conservation Endeavours in Latin America

According to UNEP figures, the amount of land and the number of terrestrial and marine protected areas (PA) designated nationally has grown exponentially around the globe. In a comparatively short period from 1990 to present, the Latin America and Caribbean (LAC) region has witnessed a 100% increase in land set aside for protection. To date, 21.2% (global average 11.6%) of the land is protected in some 4,700 parks and reserves. Among them, one of the 20 largest nationally designated protected areas in the world is to be found: Archipiélago de Colón (Galápagos) in Ecuador. The proportion of protected land is at present the highest for all developing regions worldwide and exceeds the overall percentage for the so-called developed countries by 6.8% (ICSU-LAC 2009).

Biosphere reserves represent a protection category that is designed to combine approaches to both conservation and sustainable development. Since 1977, the UNESCO's Man and the Biosphere Programme has been responsible for the development and establishment of biosphere reserves worldwide. Although they fall under national sovereign jurisdiction, the reserves stand for sharing experience and ideas on national, regional, and international levels within the World Network of Biosphere Reserves (Table 22.2). There are currently 553 approved sites worldwide in 107 countries, among them four in Ecuador (Galápagos, Yasuní, Sumaco, and Podocarpus-El Condor; Table 22.3).

In addition to national protected areas, the LAC region possesses around 250 Ramsar sites and 130 National Heritage sites, some of which overlap spatially with national parks and other reserves. In view of these important numbers, it is important to stress the fact that protected areas cannot solely be looked upon as mere reservoirs of natural resources, but also as territories that safeguard the rights of existence of nature (see Sect. 22.6).

In an attempt to bring together all the different actors, the second Latin-American Congress of National Parks and Protected Areas, which took place in San Carlos de Bariloche (Argentina) in 2007, attracted more than 2,200 participants. A major outcome of this congress was the adoption of an extensive document, the Bariloche Declaration. Although criticised by some as a rather "lengthy" document, being

Table 22.2 Biosphere reserves worldwide (UNESCO 2009)

Region	Number of biosphere reserves	Number of countries
Africa	52	22
Arab States	261	13
Asia and the Pacific	113	22
Europe and North America	258	31
Latin America and the Caribbean	104	19

Table 22.3 Protected areas in Ecuador (according to Triana 2009)

Protected areas of Ecuador	Number of areas	Area km^2	% of Ecuador's territorial area
Total area of nationally recognised protected areas	105	205,516	15.1%
Terrestrial (% of Ecuador's Terrestrial Territorial Area)	104	72,124	25.4%
Marine and Littoral Protected Area	3	133,392	
Nationally recognised protected areas greater than 1,000 km^2	23		
Nationally recognised protected areas greater than 10,000 km^2	1		
Wetlands of International importance (Ramsar Sites)	12	1,708	
UNESCO-MAB Biosphere Reserves[a]	3	173,151	

[a] Podocarpus-El Condor (approved in 2007) not yet included

Note that some protected areas include both terrestrial area and marine area "broad, but not deep" (McElhinny 2007), the scope of this congress reached far beyond protected areas management. It covered, among other things, themes such as payment systems for environmental services, the role of indigenous knowledge and people in conservation activities, and biodiversity science.

Furthermore, the aspect of financial sustainability was raised by demonstrating that, if divided by the 300 million ha of existing protected areas (PAs), the sum of money available for Latin-American PAs only equals about US $2.3 per ha. Following McElhinny (2007), this is far below the average for some developed countries, e.g. USA ($25.6/ha); Canada ($11/ha), and New Zealand ($9.6/ha). As a consequence, to promote the well-being of Latin-American society – within, but also outside protected areas – it is important to think simultaneously about compensation for environmental services and poverty alleviation (Swallow et al. 2009). In Ecuador, the RISAS network (Red de Interesados e Interesadas en Servicios Ambientales en Ecuador) is working towards this goal. Ecuadorian case studies have so far focused on PAs; however, they have also involved small municipalities, organisations, and communities and have addressed other issues, such as carbon sequestration. The set-up systems are still weak as there is limited financial sustainability and high dependence on external funds, and not all service users could be integrated, as incorporation of the service users is voluntary, not mandatory (cf. Poats 2007).

22.4 Striking New Paths for Biodiversity Protection in Latin America

Although a remarkably large area of Latin America is designated as PAs, this kind of canopy protection cannot be the only true solution for halting the loss of biodiversity. Indeed, if people are to appreciate the true significance of biocultural diversity, nothing less than a cultural change has to take place, to be understood as "a form of co-evolution between cultural information and the social and natural environment" (Smith 2001). For this purpose, alternative protection approaches have to be considered which take into account both the predominant part of the continent which does not enjoy protection of any kind and the cultural diversity in this region, one of the most prominent worldwide (ICSU-LAC 2009).

As many protected areas overlap with indigenous territories, this provides interesting opportunities both in terms of co-management and enriching the concepts and tools of conservation and helping to build sustainable societies. Not only in countries with large indigenous populations (e.g. Bolivia, Ecuador, Peru, Guatemala, and Mexico), but also in countries where they are a minority (Argentina, Brazil, Colombia, Costa Rica, Chile, and Venezuela) their relevance for effective conservation of ecosystems and the co-management of protected areas is increasingly appreciated (Guerrero 2009). Sites managed under this rather new form of resource management are termed Community Conserved Areas or

Indigenous and Community Conserved Areas (ICCAs) and have been acknowledged by the IUCN and Parties to the Convention of Biological Diversity (cf. Kothari 2006; www.iccaforum.org).

This does not necessarily mean that all activities and practices developed locally may foster biodiversity by any means, nor that poor management does not take place; however, the worldviews of many traditional societies were conducive to the development of practices and skills that manage ecological integrity in sustainable ways. Hence, the loss of one aspect (e.g. locally appropriate knowledge and practices) could cause a concomitant loss of the other (e.g. ecological resilience) (cf. Pretty et al. 2009). Furthermore, several analyses have shown that the share of indigenous protected tropical forest is more than noteworthy (e.g. 12.2% in Latin America; cf. Nelson and Chomitz 2009). Even more importantly, indigenous reserves have proven to be more effective both in terms of habitat and of climate protection than all other protected areas, with the exception of those that are highly protected (Ricketts et al. 2010; Naughton-Treves et al. 2005; McElhinny 2007; Waylen et al. 2009).

A UNDP Regional Programme for Latin America and the Caribbean (LAC) (full name: “Biodiversity and Ecosystems: Why these are Important for Sustained Growth and Equity in Latin America and the Caribbean”) has been created to convince policy- and decision makers in the region to invest in and maintain biodiversity and ecosystem services. The initiative is organised in partnership with the UN Environment Programme (UNEP), UN Economic Commission for Latin America and the Caribbean (ECLAC), and the Secretariat for the Convention on Biological Diversity (CBD). From 2008 to 2011, a report will be compiled to examine, among other things, the following issues: financial and economic benefits and costs to countries from sustainable ecosystem management; the contribution of biodiversity and ecosystems to sectoral production and outputs; the economic value of biodiversity and ecosystems; and the role of biodiversity and ecosystem services in promoting growth and equity.

With a view to integrating the manifold experiences and views of the various LAC nations, a series of consultations was initiated across the region in August 2009. The Ecuador consultation took place in Quito in November 2009 and was attended by participants from national, state, and local governmental bodies; conservation groups; academic and scientific groups; and representatives from the Amazonian and highland regions of Ecuador. To prepare a national report on the role of biodiversity and sustainable development in the long-term economic wellbeing of the nation and the region, the participants discussed several case studies and identified strategic sectors (agriculture, tourism, forestry, water, coastal and marine resources, and biocommerce/biotechnology), and attempted to find linkages between ethics, equity, and economy within these topics. Furthermore, emphasis was laid on the role of spiritual values, ancestral knowledge and, with regard to a dissemination strategy, the need for communicative approaches aiming to connect biodiversity, daily life, and culture.

The intention of the final report is not only to contribute to national policies but also to global and regional key policy. Measures for safeguarding this purpose encompass supervision and guidance by a Commission for Biodiversity, Ecosystems, Finance and Development composed of regional political leaders, ecological and economic experts, and civil society representatives.[1]

22.5 Awareness Raising and Communicative Efforts in Latin America

If “knowledge of a country’s species and ecosystems by its citizens also fosters national pride and culture, as well as a sense of curiosity for discovery and the unknown” (ICSU-LAC 2009, p. 89), then the question arises as to how to motivate and educate people towards this rather ambitious goal. Both education and communication at the science/policy interface, although they are rated as important success factors to strengthen biodiversity conservation, are largely neglected, if not ignored. According to Rodriguez et al. (2007), only 4% of the US$ 3.26 billion invested in Latin-American biodiversity conservation between 1990 and 1997 was spent specifically on capacity building. With respect to safeguarding tropical forest biodiversity, Brooks et al. (2009), similarly, state that this area receives only “a small fraction of outreach efforts”, which in turn results in frustrating attempts to measure success and thus improve conservation measures (Bride 2006). Some say that if science continues to put emphasis on what to save, rather than how to do so, and, in doing this fails to relate the wealth of nature to people’s everyday life, it inevitably creates the impression that it is cataloguing deck chairs on the Titanic (Shanahan 2008).

On the other hand, it is only fair to say that there are initiatives to resolve these shortcomings. Particularly with regard to protected areas, there are a number of noteworthy efforts. For instance, communication plays a central role in the Madrid Action Plan for Biosphere Reserves (2008–2013) (UNESCO 2008). To achieve the vision and mission of the MAB Programme, approval and implementation of the defined targets will be evaluated in 2010 and 2013. It will be interesting to see if, and how, biosphere reserves have developed and launched targets, such as an integrated information and communication strategy (Target 3). Another initiative worth mentioning is the First Joint commission meeting of the World Commission on Protected Areas (WCPA; with 1,400 members in 140 countries) and the IUCN’s Commission on Education and Communication (CEC; encompasses about 600 expert practitioners). The meeting took place in Ecuador in May 2009 and this collaborative push forward produced a decision to work on the following fields: knowledge management; raising the visibility/credibility of PAs; communication strategy; and capacity building at all levels for policy, decision makers, PA management, and leadership at the grassroots (IUCN-CEC and WCPA 2009).

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[1] IISD reports: http://www.iisd.ca/process/biodiv_wildlife.htm#undp_lac.

In the long run, it will be crucial to fill all well-meaning intentions with life and not to perpetuate maladjustments. The CEC needs to define goals and the financing of them in specific and targeted manners. To “walk the talk” in this case means providing the human and financial resources to undertake effective work (MEA 2005).

22.6 New Approaches for Sustainable Development and Biodiversity Conservation in Ecuador

In 2006, Rafael Correa was elected President of the Republic of Ecuador. He was re-elected to a second term in April 2009. In January 2007, a referendum on establishing a Constituent Assembly to rewrite the Ecuadorian constitution was called by President Rafael Correa. The referendum was held on 15 April 2007 and a large majority voted in favour of establishing the Constituent Assembly. In November 2007, the assembly began its work, and the new constitution was finally approved in a referendum in September 2008.

In the process of drafting the new Ecuadorian constitution, two topics were discussed intensively: the indigenous concept of “Sumak Kawsay” (“Good Living”) and the idea of establishing rights of nature. Finally, both concepts were incorporated in the new Ecuadorian constitution.

22.6.1 Sumak Kawsay

Sumak Kawsay is a concept of the indigenous peoples from Bolivia, Ecuador, and Peru. In the Quechua language, it means good living (“Buen Vivir” in Spanish). *Sumak Kawsay* means harmony, dialogue, and equity among human beings as well as between humankind and nature; the sustainable use of natural resources (the planet is seen as “Pachamama” – “Mother Earth”); the maintenance of ecological systems and cycles; equity, solidarity, and dignity; respect for diversity; ethics of responsibility; and harmonious life instead of linear development (cf. Acosta 2009a, b; Boff 2009; Quirola Suárez 2009; Roa Avendaño 2008). “The good living encourages us to consume no more than what the ecosystem can bear” (Boff 2009; translated from Spanish by the authors). It is a “conception of life far removed from the most cherished elements of modernity and economic growth: individualism, the search for profit, the cost–benefit relationship as a social axiom, the use of nature, strategic relations between human beings, the total commodification of all spheres of human life, the inherent violence of consumer selfishness, etc.” (Davalos 2009).

Apart from the members of the Constituent Assembly, many representatives of civil society organisations, such as environmental NGOs and indigenous organisations, as well as scientists, participated in the debate about *Sumak Kawsay* during the process of drafting the new Ecuadorian constitution, enriching the discussion with their ideas and visions. The result was that the principle of *Sumak Kawsay* was incorporated not only in specific articles of the new Ecuadorian constitution, but also can be seen as the foundation of the whole constitution, as an overall concept for creating a sustainable society (cf. Acosta 2009b). Article 14 of the constitution (2008) states (translated from Spanish and italicised by the authors):

> "Art. 14.- The right of the population to live in a healthy and ecologically balanced environment which guarantees sustainability and the good living, *Sumak Kawsay,* is recognised. The preservation of the environment, the conservation of the ecosystems, the biodiversity and the integrity of the genetic patrimony of the country, the prevention of environmental damage and the recuperation of degraded natural spaces are declared to be of public interest."

Elements of *Sumak Kawsay* which have been established in the constitution and which are seen as playing a role in sustainable development in Ecuador are in particular: solidarity economy; equity; gender equality; quality of life; education, health, and water access as human rights; participative democracy; decentralisation; fight against corruption; peace; cultural diversity and interculturality; food sovereignty; rights of nature; nature conservation; sustainable use of natural resources; and access to the natural resources for all human beings and communities (Acosta 2009b; Carpio Benalcázar 2009; Quirola Suárez 2008). A crucial aim is to transcend the economy based on the extraction of primary resources, especially petroleum (cf. Larrea 2009 about the negative impacts of the "petroleum economy"), and to develop a "post-petroleum economy", hence a sustainable economy which can be characterised as ecological and fair (Acosta 2009b):

> "The economic system is social and solidary; it recognises the human being as subject and end; it tends toward a dynamic and equal relationship between society, state and market, *in harmony with nature*; and its objective is to guarantee the production and reproduction of the material and immaterial conditions that facilitate the good living." (Art. 283, Ecuadorian Constitution 2008; translated from Spanish and italicised by the authors)

22.6.2 Rights of Nature

The idea of granting rights to nature is not new. It has been discussed for decades in different parts of the world, for instance by the jurists Christopher Stone (1972) from the USA and Godofredo Stutzin (1984) from Chile (cf. Melo 2009).

In the new Ecuadorian constitution, nature has been recognised as a subject of rights. The constitution includes a novel set of articles that appear to be the first in any constitution granting inalienable rights to nature. The section about rights of nature was written in cooperation with the Community Environmental Legal Defense Fund, based in Chambersburg, Pennsylvania, which has helped individual communities legislate similar rights of nature, and the Ecuadorian Pachamama Foundation. The importance of granting rights to nature can be justified with the existing destruction of the environment, the concept of environmental justice as well as the necessity to regulate economic processes and to prevent negative ecological impacts of these processes (Gudynas 2009).

The rights of nature have been coined in the constitution of Ecuador (2008) in the following terms (translated from Spanish and italicised by the authors):

> *Seventh Chapter: Rights for Nature*
>
> "Art. 71.- Nature or Pachamama, where life is reproduced and exists, has the *right to exist, persist, maintain and regenerate its vital cycles, structure, functions and its processes in evolution*. Every person, community, people, or nationality, will be able to demand the compliance with the rights of nature before the public organisms. [. . .] The State will motivate natural and legal persons, as well as collectives, to protect nature; it will promote respect towards all the elements that form an ecosystem."
>
> "Art. 72.- Nature has the *right to restoration*. [. . .] In the cases of severe or permanent environmental impact, including those caused by the exploitation of non-renewable natural resources, the State will establish the most effective mechanisms for their restoration, and will adopt suitable measures to eliminate or mitigate any harmful environmental consequences."
>
> "Art. 73.- The State will apply *precautionary and restrictive measures* in all the activities that can lead to the extinction of species, the destruction of ecosystems or the permanent alteration of natural cycles. The introduction of organisms and organic and inorganic material that can irrevocably alter the national genetic patrimony is prohibited."
>
> "Art. 74.- The persons, communities, people and nationalities will have the *right to benefit from the environment and form natural wealth* that will allow the *good living*. The environmental services cannot be appropriated; their production, provision, use and exploitation will be regulated by the State."

This recognition of the rights of nature has juridical as well as political implications, because nature becomes a subject of administrative and judicial protection (Espinosa 2009). "Conceiving nature as a subject of rights breaks with the traditional paradigms which were constructed on the basis of Occidental visions" (Acosta 2009a, p. 15; translated from Spanish by the authors), because in general rights are only granted to persons. Thus, assigning rights to nature is quite a ground-breaking approach.

Against the background of the rights established in the Ecuadorian constitution, nature has to be seen as a subject with legal rights and legal legitimacy and no longer only as an ensemble of objects which can be owned by everybody (Acosta 2009a). This shift of paradigm is linked to biocentric ethics and the idea that nature has an intrinsic value which is independent of its value for human beings (cf. Acosta 2009a; Gudynas 2009).

The rights of nature are a crucial element of *Sumak Kawsay*, because they create the basis for a harmonic coexistence between human beings and nature and hence for nature conservation. The idea is that establishing such rights will lend more importance to nature, prevent environmental damage, and create environmental awareness, among other things (Acosta 2009a). By establishing rights of nature, political responsibilities for nature conservation are created, and moral obligations for protecting the ecosystems, conserving endangered species, and avoiding environmental pollution are determined (Gudynas 2009).

22.6.3 *Biodiversity Conservation in the New Ecuadorian Constitution*

Based on the concept of *Sumak Kawsay* and the rights of nature, the Ecuadorian Constitution (2008) mentions and establishes the importance of biodiversity conservation in different articles, for instance in the following (translated from Spanish and italicised by the authors):

> "Art. 57.- The following collective rights are recognised and guaranteed for the indigenous communes, communities, peoples and nations [. . .]: 8. To conserve and promote their practices of the use of *biodiversity* and the natural environment. The State will establish and execute programmes, with the participation of the community, to ensure the conservation and sustainable use of *biodiversity*."
>
> "Art. 259.- With the intention to conserve the *biodiversity* of the Amazonian ecosystem, the central State and the decentralised autonomous governments will adopt policies of sustainable development [. . .]."
>
> "Art. 395.- The Constitution recognises the following environmental principles: 1. The State will guarantee a sustainable model of development, environmentally balanced and respectful of the cultural diversity, which conserves the *biodiversity* and the natural regeneration capacity of the ecosystems, and ensures the satisfaction of the needs of the present and future generations."
>
> "Art. 400.- The State will execute the sovereignty over *biodiversity* administration and management of which will be realised with intergenerational responsibility. The conservation of *biodiversity* and all its components, in particular agrarian and wild *biodiversity* and the genetic patrimony of the country, are declared to be of public interest."

It is thus evident that the new Ecuadorian constitution creates a broad and extensive basis for biodiversity conservation policies.

Corresponding policies and strategies have already been included in the National Plan for the Good Living (Plan Nacional para el Buen Vivir, PNBV), especially in objective 4 "To guarantee the Rights of Nature and facilitate a healthy and sustainable environment". The analysis of the current situation and the legal necessities has already begun to make this objective a reality. This is particularly important, because the areas with most significant biodiversity are located in the Amazon region where oil extraction, in particular, poses a major threat. The most important zones requiring protection are the provinces Napo, Orellana and Sucumbios where the Biosphere Reserves Sumaco and Yasuní are located (Plan Nacional para el Buen Vivir 2007–2010 and 2009–2013, http://www.senplades.gov.ec).

22.7 Putting the Constitution into Force: The Yasuní-ITT Initiative

Based on the concepts of *Sumak Kawsay* and the rights of nature, the Yasuní-ITT initiative[2] has been developed to take the initial steps to move from an oil-based economy to a new sustainable development model.

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[2] http://www.yasuni-itt.gov.ec.

With this initiative, which was presented for the first time by the Ecuadorian president Rafael Correa before the United Nations in September 2007, Ecuador is committed to leaving underground 20% of its proven oil reserves (850 million barrels), located in the ITT (Ishpongo-Tambococha-Tuputini) oil fields within the Yasuní National Park, one of the most important and diverse biological reserves in the world (major ecosystem type: tropical humid forests, area: 1,682,000 ha) (cf. Amazon Watch 2008; Larrea 2009; Larrea et al. 2009; Oilwatch 2007). The reserve has an estimated 2,274 tree and bush species, 593 bird species; 80 bat, 150 amphibian, and 121 reptile species as well as 4,000 vascular plant species per million hectares; and about 100,000 insect species per hectare. “The park has the highest density of amphibious, mammal, bird, and plant species in the Amazon region” (Larrea et al. 2009, p. 13; cf. Bass et al. 2010) (Fig. 22.1).

Fig. 22.1 The Yasuní National Park in Eastern Ecuador (Burzio 2008)

In return for not exploiting the oil fields within the Yasuní National Park, Ecuador expects from the international community a contribution of at least half the revenue which Ecuador would have received by extracting the oil; this is to finance the creation of a capital fund to be administered by an international trust, with the participation of the government, Ecuadorian civil society, and donors. It is intended that the contributions to the international cooperation fund will come from two main sources: voluntary contributions (from governments of other countries, international multilateral organisations, civil society organisations, companies, and citizens worldwide) and transactions in the carbon market (cf. Larrea 2009; Larrea et al. 2009). "In exchange for the contributions, the Ecuadorian State will guarantee to maintain ITT oil reserves underground indefinitely. The government will issue guarantee certificates for the nominal value of the compensations [...], up to the quantity of 407 million tonnes of carbon dioxide not emitted. The real backing for the guarantees will be the value of the investments made by the capital fund" (Larrea et al. 2009, p. 4).

The fund's capital will be invested, in particular, for the development of renewable energy sources, nature conservation as well as social development, as part of a strategy which aims at consolidating a new model of sustainable human development in Ecuador. The project aims at combating global warming, conserving the biodiversity in the Yasuní National Park, and permitting the survival of the voluntarily isolated indigenous peoples who live in the ITT area (cf. Larrea 2009; Larrea et al. 2009; Oilwatch 2007).

To date, different European governments have stated support. The German government has agreed to contribute funds, but the conditions for this support have not been defined yet. The discussion of the details of the capital fund's implementation at the UN Climate Change Conference in Copenhagen in December 2009 led to a conflict between President Correa, the coordination board of the Yasuní-ITT initiative and the United Nations which created some confusion as to the future of the project. In February 2010, Correa declared that he is willing to continue the project. In the beginning of August 2010, the Ecuadorian Vice-President Lenín Moreno and Rebeca Grynspan from UNDP (United Nations Development Program) signed an agreement for the creation of an international trust fund for the Yasuní-ITT initiative. This agreement can be seen as an important step forward for the initiative.

22.8 Conclusions

Latin America is characterised by a very high level of biodiversity. However, this biological diversity is under continued threat from socio-economic development. Thus, it has become evident that biodiversity conservation is not possible without sustainable development, i.e. a development which aims at both societal welfare and environmental protection. Biosphere reserves combine approaches to biodiversity conservation and sustainable development, because they facilitate sustainable economic activities which are ecological on the one hand, and, on the other hand, can provide means of livelihood for the population. However, they are restricted to particular areas. In Ecuador, for instance, there are four Biosphere reserves, but in the rest of the country the rainforest is cut down, the rivers are polluted, etc.

Against this background, it has become apparent that new approaches are needed which involve larger areas, consider the cultural diversity, provide opportunities for co-management involving indigenous communities, and thus contribute to the emergence of sustainable societies. Furthermore, it has been shown that communication and capacity building are needed to support conservation endeavours.

Ecuador has recently incorporated the idea of *Sumak Kawsay* and the rights of nature in its new constitution. Thus, creating harmony between human beings and nature as well as biodiversity conservation have been institutionalised as constitutional goals. As the first country in the world which guarantees rights for nature in its constitution, Ecuador breaks with traditional paradigms and recognises the intrinsic value of nature. The new Ecuadorian constitution means significant progress for the national, and also the international conservation discourse. The Yasuní-ITT initiative can be seen as a pilot project for implementing the idea of *Sumak Kawsay* as well as creating a "post-petroleum economy" and a sustainable society. Furthermore, it can be understood as a contribution to achieving global environmental justice. Additionally, the debates about *Sumak Kawsay* and the rights of nature as well as the Yasuní-ITT initiative have led to more societal awareness about issues of biodiversity conservation and sustainable development.

In conclusion, it can be said that the approaches discussed in Ecuador are innovative; they represent a paradigmatic shift and show new opportunities for reconciling economic development and biodiversity conservation. Nevertheless, problems in the legal and political implementation of the new approaches are already apparent. Weak public institutions, for instance, impede effective environmental policy and management. Moreover, economic interests are still very strong in Ecuador; whether the constitution remains a mere discourse or whether it results in truly sustainable development will depend largely on the role civil society plays. Hence, the Yasuní-ITT proposal can be seen as a litmus test for the political and legal strength of the new Ecuadorian constitution.

So far there is no research on the implementation process of the described constitutional goals, and long-term impacts will have to be analysed. It remains open whether *Sumak Kawsay* and the rights of nature will eventually make a real difference for "Pachamama".

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Chapter 23
When Hotspots Meet: The Galápagos Islands: A Hotspot of Species Endemism Based on a Volcanic Hotspot Centre

Sebastian Steinfartz

Abstract The evolution of endemic species on the Galápagos archipelago, a geological setting of remote volcanic islands that have never been in touch with any continental landmass, has influenced as no other specific natural system modern biology. This chapter is aimed to provide an overview of how species endemism on this unique system is linked to general geological mechanisms, is distributed across islands and broken down exemplarily to well-studied emblematic species groups such as giant tortoises and Darwin finches, but also to less well known, but highly fascinating species complexes such as marine and land iguanas as well as sea lions. A concluding perspective on existing human and naturally induced threats, but also on practised successful measures against introduced and alien species highlights that endemism of the Galápagos is in conservation peril.

23.1 Introduction

Hotspots of terrestrial biodiversity and species endemism are classically found in areas of continental tropical rain forests in the equatorial regions of Middle and South America, Central Africa and South East Asia as well as on major tropical island complexes such as the Caribbean, Madagascar and the Indian Ocean islands. Remote tropical islands, on the other hand, that were purely built and shaped by volcanic activity and have never been in touch with any continental land mass during their geologic history represent a completely different setting and possible source of high species endemism. The most prominent representatives of such island systems are the Hawaiian Islands, located roughly 3,400 km west of the nearest mainland coast of Central America, and the Galápagos islands that belong

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to the state of Ecuador and are located roughly 1,000 km west of the South American continent. Although rather little is known about the processes and mechanisms that have shaped species diversity and endemism in the hotspot centres located on the mainland or large island complexes that have been part of former continents (e.g. Madagascar), we can infer that the underlying basic mechanisms and conditions that have resulted in the observed species diversity and degree of endemism of remote, volcanic islands must have been basically different. First, in contrast to the situation on the main land, an upper limit for the temporal origin of species assemblages founded by colonization processes can be relatively correctly inferred from the emergence age of respective volcanic islands. Second, due to their geographic remoteness from possible sources on the mainland, founder events leading to a successful establishment of species-specific lineages across oceanic, volcanic islands must have been comparably rare. Indeed, many species assemblages of terrestrial vertebrates on the Galápagos archipelago can be traced back to a single founder event from the mainland. Finally, the geographic isolation of remote oceanic islands allowed for the survival of "ancient" species (e.g. giant tortoises) that have been displaced or outcompeted by novel evolutionary lineages (e.g. mammals) being more successful.

This chapter is aimed to provide an overview on patterns of species endemism of the Galápagos archipelago; one of the world's most famous and intensively studied system of remote, oceanic islands of volcanic origin. After introducing the general geology of this system, I will provide a short overview on general species endemism of the archipelago before focusing on specific examples of terrestrial and marine vertebrate species. Besides presenting data on well-known systems such as giant tortoises and Darwin finches, I will try to put a special emphasis on presenting new and exiting insights from less well-covered species such as marine and terrestrial iguanas and sea lions. Concluding, I will point out specific threats for the endemic fauna and flora of this unique natural system at the end of this chapter.

23.2 Geology of the Galápagos Archipelago

The Galápagos archipelago consists of 13 major islands (>10 km^2), six smaller islands and numerous islets (see Fig. 23.1). The islands have been produced by a volcanic hotspot that lies beneath the Nazca plate, which is travelling in an eastward direction. Consequently, island ages generally decrease from east to west, and the oldest islands found nowadays are San Cristóbal with an estimated age between 2.35 and 4.04 million years and Española with 3.31–3.54 million years (Cox 1983) in the south-east of the archipelago. The geologically youngest and most western island Fernandina, on the other hand, overlies the volcanic hotspot centre most closely and is the most active volcano in the archipelago. It has an estimated age of only 35,000 years based on age estimates of exposed lava flows on this island (Kurz et al. 2005). However, hotspot activity and the continuous production of oceanic islands in that region has been started long before than can be inferred from the age

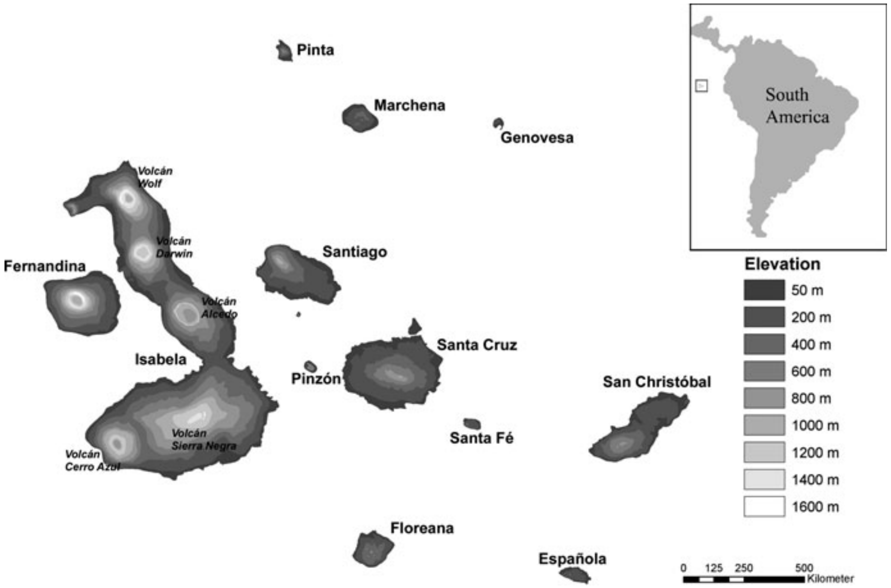

Fig. 23.1 General location of the Galápagos archipelago (*inlet*) and major islands. Isabela might have started from five distinct volcanoes and merged later to one continuous island (see text for explanations)

of the current oldest/most eastern islands in the archipelago. The analysis of submarine sea mounts to the south-east of the present archipelago suggests that the hotspot centre has been already active since 80–90 million years ago (Christie et al. 1992). Islands as born by the activity of the hotspot in the west of the archipelago appear above the sea level, are transported like on a conveyor belt to the east and finally doomed to sink into oblivion. Thus, the Galápagos archipelago has to be seen as a rather dynamic system that is characterized by the continuous rise of new islands and submergence of older ones. Naturally, this rise and submergence of islands also impacted the biogeography of many species and the specific evolution of species diversity on the Galápagos. This correlation can be nicely exemplified for the split of marine from terrestrial iguanas in the archipelago: molecular dating suggests that both species must have split more than ten million years ago on now sunken islands (Rassmann 1997).

Another important aspect of island dynamics of this unique system can be observed by looking at the largest island of the archipelago, Isabela. At a first glance, Isabela nowadays forms one continuous island mass with six distinct volcanoes (see Fig. 23.1). Indeed, it is very probable that each of these volcanoes started off as a separate island and was connected to its nearest neighbour by additional lava flows through time. Naumann and Geist (2000) estimated emergence ages of volcano Cerro Azul to 350,000 years, for Sierra Negra to 535,000 years and to 313,000 years for volcano Alcedo. The formation of Isabela by separately arisen volcanoes is also in line with observed species diversification of giant tortoises on this island. Most of

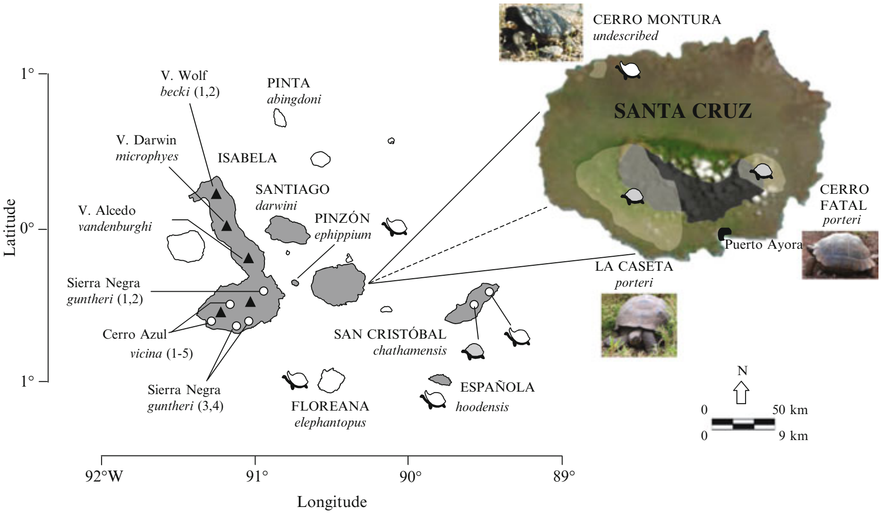

Fig. 23.2 Distribution of remnant Galápagos giant tortoises throughout the archipelago and on Santa Cruz. *Shaded islands* indicate the presence of extant tortoise populations and *italized names* represent current subspecific designations; island names indicated in *all capitals*, with distinct populations on Isabela specified by name; *triangles* represent volcanoes and *circles* indicate sampled populations throughout the archipelago. *Shaded* and *unshaded* tortoise caricatures signify "domed" and "saddleback" morphologies, respectively. The current distributions of tortoises (*shaded yellow*) and the agricultural corridor (*shaded black*) on Santa Cruz are plotted on a satellite map (MODOS Rapid Response Project, NASA/GSFC). Scale bar specified for the Galápagos archipelago (*above*) and Santa Cruz (*below*) (from Russello et al. 2005)

the volcanoes inhabit also distinct taxa of Galápagos giant tortoises (e.g. Russello et al. 2005 and Fig. 23.2).

23.3 A Short Overview on Species Diversity on the Galápagos

The climate of the Galápagos islands is relatively arid and topographic diversity of the islands compared with other volcanic oceanic islands such as Hawaii is lower resulting in a comparable low overall habitat diversity. Semi-terrestrial and terrestrial habitat zones as characterized by plant communities can be divided into the littoral or coastal zone (including beaches, lagoons and mangroves) followed by the arid zone, which is the most extensive habitat type on the islands with the greatest number of endemic species and characterized by deciduous trees and shrubs. The coastal zone is followed by the transition zone (intermediate in character between the arid zone and the *Scalesia* zone, but dominated by different species, resulting in a diverse, mainly deciduous dense forest), the *Scalesia* zone, comprising lush evergreen cloud forest dominated by *Scalesia pedunculata*, and the open pampa zone consisting largely of ferns, grasses and sedges (Jackson 1993).

More than 550 species of native (i.e. species that are generally agreed to have arrived naturally or evolved in the Galápagos including also endemic species; see Table 23.1) vascular plants can be found throughout the archipelago (Acharya 2000; Tye 2006; Guézou et al. 2010). By increasing their number up to 870 species (Guézou et al. 2010) introduced and alien plant species nowadays already outnumber native species by a relation of 1.57:1. Accordingly, more than 1,400 plant species belonging to five distinct taxonomic divisions (Lycopodiophyta, Pteridophyta, Cycadophita, Pinophyta and Magnoliophyta) inhabit the archipelago. Until 2001 a total of 2,289 terrestrial invertebrate species were registered, of which more than half are supposed to be endemic to the Galápagos islands (Herrera and Roque-Álbelo 2010). One of the most outstanding examples concerning number of species and degree of endemism concerns the radiation of land snails (genus *Bulimulus*) with 71 described species that have colonized all terrestrial habitat zones of the archipelago except for the littoral (or coastal) zone (Parent and Crespi 2006).

Overall, the terrestrial fauna of the Galápagos is dominated by vertebrate species belonging to reptiles, birds and mammals that have diversified to varying degrees after successful colonization into species complexes. Seven reptile lineages were

Table 23.1 Overview of species diversity of plants and selected animal groups on the Galápagos archipelago

		Estimated number of species	Comments
Plants		>1400[a,b]	
		ca. 552 native taxa[a,b]	*Native taxa*: species that are generally agreed to have arrived naturally or evolved in the Galápagos (*native* here includes also endemics)
		ca. 870 alien or introduced taxa[a]	
Animals	*Terrestrial invertebrates*	>2300 species are currently described, of which half is endemic to the Galápagos[c]	Until 2007 a total of 490 insect and 53 other terrestrial vertebrate species were regarded as introduced[c]
	Amphibians	Two introduced frog species[d]	
	Reptiles	51 species are recorded for the Galápagos, of which 38 are endemic and native[e]	Five species are currently known to be extinct and one is extinct in the wild (*Geochelone abingdoni*)[e]
	Birds	178 species are recorded for the Galápagos, of which 56 are native[f]	
	Mammals	56 species recorded for the Galápagos, of which 16 are native[g]	8 species are extinct, of which 5 became extinct before humans arrived and are only reported by fossils[g]

According to [a]Guézou et al. (2010), [b]Tye (2006), [c]Herrera and Roque-Álbelo (2010), [d]Jiménez-Uzcátegui et al. (2010a), [e]Jiménez-Uzcátegui et al. (2010b), [f]Jiménez-Uzcátegui et al. (2010c), [g]Jiménez-Uzcátegui and Snell (2010) able to colonize the archipelago and four of them (tortoises, lava lizards, snakes and leaf-toed geckos) diversified into distinct numerous species or recognizable subspecies across the islands. The best reptile species-system studied so far on the Galápagos comprises giant tortoises (genus *Geochelone*) that have not only diversified between islands in different lineages, but also within (e.g. on Isabela; see also Fig. 23.2). Furthermore, their diversification is not only mirrored on the genetic level as revealed by nuclear and mitochondrial DNA markers, also on the morphological level tortoise species comprise distinct shell shapes (e.g. domed versus saddlebacked carapaces; see Fig. 23.2) that are adapted to different habitat types.

Up to 178 distinct bird species can be seen on the Galápagos, of which 56 are supposed to be native (Jiménez-Uzcátegui et al. 2010a, b, c; see Table 23.1). Besides the already mentioned radiation of Galápagos bulimulid land snails the radiation of Darwin's finches into 14 distinct species is the only other well-acknowledged case of adaptive radiation on the Galápagos. The mockingbirds (genus *Nesomimus*) as represented by four species constitute the next largest group of endemic species with all four species occurring in the littoral and arid zones. There are only four single-island endemics in Galápagos, these being *Camarhynchus pauper* and *Nesomimus trifasciatus* (on Floreana and satellites), *N. melanotis* (on San Cristóbal) and *N. macdonaldi* (on Española), the remaining species generally being found on three or more islands. Six seabird species (the Galápagos Penguin, *Spheniscus mendiculus*; the waved Albatross, *Diomedea irrorata*; the Galápagos Petrel *Pterodroma phaeopygia*; the Galápagos Cormorant, *Phalacrocorax harrisi*; the lava Gull, *Larus fuliginosus* and the swallow-tailed Gull, *Creagrus furcatus*) are endemic breeders on the archipelago (BirdLife International 2003).

Compared to the number of reptile and bird species only rather few mammal species (two bat and several rat species) naturally colonized the Galápagos archipelago. Out of these, only the rice rats diversified further into ten distinct species (genera Oryzomys, Nesoryzomys and Megaoryzomys). Marine mammals are represented by two endemic species, the Galápagos sea lion (*Zalophus wolebaeki*) and the Galápagos fur seal (*Arctocephalus galapagoensis*). Other mammal species such as goats, cats and dogs have been introduced to the islands by settlers and now it is one of the biggest threats to the endemic fauna in this area.

23.4 Examples of Species Endemism in the Galápagos Archipelago

In this section, I will focus on two outstanding and well-documented examples of species endemism on the Galápagos, the giant tortoises and Darwin's finches as well as on two less known species systems – land and marine iguanas and the Galápagos-sea lions – for which new and exciting data have been gathered in the very recent past.

23.4.1 Galápagos Tortoises

Giant tortoises (*Geochelone nigra*) undoubtedly belong to the most emblematic species group of the Galápagos-islands and symbolize as no other species the historic and present threat to endemism on the Galápagos archipelago. Worldwide, they represent the largest extant terrestrial chelonians and form a monophyletic species assemblage derived from a mainland South American lineage that radiated within the archipelago in several distinct evolutionary units (see Fig. 23.2). Fifteen formally described taxa of giant tortoises are recognized, of which only 11 are still remnant and highly threatened by anthropogenic activities, particularly by the spread of non-native species and habitat destruction. Presently, tortoises can be found on islands of San Christóbal, Española, Santa Cruz, Pinzón, Santiago and Isabela. With the exception of Isabela and Santa Cruz, where several distinct taxa are found, all of the other islands are each inhabited by a distinct taxon. Patterns of colonization represented by giant tortoises are strongly in line with the chronological rise of islands. Accordingly, colonization followed a progression from geologically older islands to younger islands, also known as a general pattern of progression hypothesis (reviewed by Parent et al. 2008). The highest level of diversity is found on Isabela with currently five distinct taxa that are each more or less confined to one of the distinct volcanoes on this island (see Figs. 23.1 and 23.2). Genetic analysis suggests that colonization of younger volcanoes occurred most probably shortly after a new volcano had emerged (Beheregaray et al. 2004). That the population structure and survival of tortoises can be tightly linked to the fate of a volcano has been supported by data showing how a prehistoric volcano eruption caused a severe population decline of tortoises near volcano Alcedo on Isabela (Beheregaray et al. 2003). Although taxa of Galápagos tortoises have been mainly described on morphological grounds rather long ago, the detection of so far cryptic taxa is still today in progress. In 2005, Russello et al. identified a new taxon of giant tortoises in the north of Santa Cruz (see Fig. 23.2) that is not only quite distinct from a genetic perspective with respect to remaining tortoise populations on this island, but also from a morphological one (Chiari et al. 2009).

23.4.2 Darwin's Finches

Darwin's finches are a prime example of a system, where intense long-term scientific effort and study has unravelled the observed microevolutionary mechanisms acting in a natural population. Up to 15 distinct finch taxa can be found across the archipelago and all of them are derived from a single colonization event from South America/Carribean (see Fig. 23.3). Beside land snails of the genus *Bulimulus*, Darwin's finches represent the only other adaptive radiation that occurred on the Galápagos. During less than three million years since their arrival on the Galápagos Darwin's finches evolved adaptive differences in beak size, beak shape and body

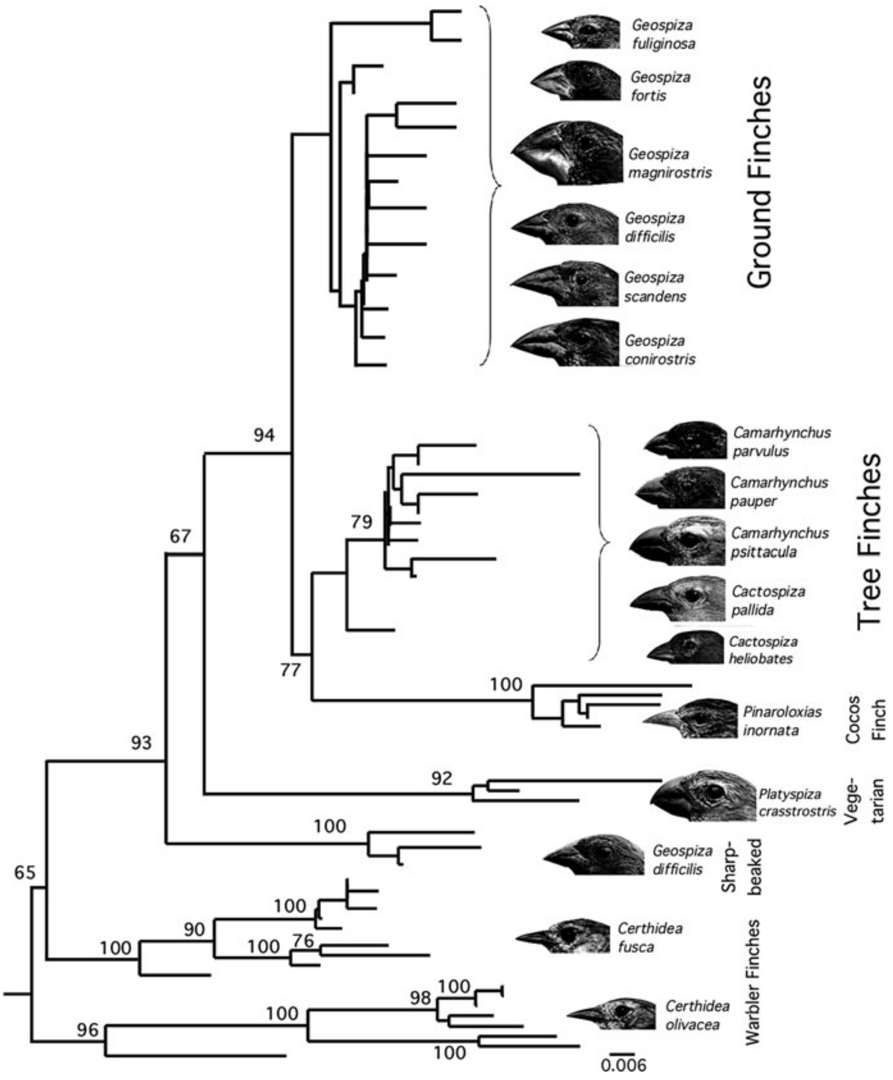

Fig. 23.3 Diversity of Darwin's finches and inferred phylogentic relationships among them based on cytochrome-b sequences. There is significant genetic structure and paraphyly among populations of sharp-beaked ground finches and warbler finches, but lack of resolution among the phenotypically distinct species of ground finches and tree finches. Photographs are proportional to actual size (from Parent et al. 2008)

size that can be otherwise found between species of distinct bird families. The adaptation of beak size and shape to different environmental conditions seems to be the driving force for the observed adaptive radiation and associated speciation processes of finches on the Galápagos. On a microevolutionary scale, the famous studies of the Grant's could show that beak size as a highly heritable trait used for food exploration shifted adaptively as a consequence of availability of different kind of seeds through climatic El Niño oscillations within generations (reviewed by Grant 2003). In turn, Podos (2001) showed that the diversification of beak morphology and body size impacted patterns of vocal signalization in finches. Such a pattern of correlated evolution among morphology and song type maybe an example how adaptively induced evolution of morphology results into song evolution that drives reproductive isolation and speciation. Even candidate genes underlying such a morphological change have been identified in this system (Abzhanov et al. 2004).

23.4.3 Galápagos Sea Lions

Sea lions on the Galápagos belong to the most abundant and conspicuous marine mammals in the archipelago and colonies of sea lions can be found at the sandy beaches across the whole archipelago. Initially, together with the Californian sea lion and the now extinct Japanese sea lion, Galápagos sea lions have been described as a third distinct species within the genus *Zalophus*. Soon after its description, however, species rank was not acknowledged and sea lions of the Galápagos were regarded as a subspecies of the Californian sea lion, *Zalophus californianus*. However, two new comprehensive genetic studies on Galápagos sea lions suggest now that sea lions on the Galápagos represent not only an endemic species, but also indicate that genetic divergence of sea lions populations found in the central and western parts of the archipelago might indicate the onset of an ongoing speciation process promoted by inter-specific niche segregation with syntopic Galápagos fur seals.

Based on sequence analysis of the mitochondrial control region (D-loop) as well as on the Cytochrome-B gene, it could be shown that lineages of Californian and Galápagos sea lions must have diverged roughly one million years ago from a common ancestral lineage. Also, the signature of genetic differentiation on the nuclear level between Galápagos and Californian sea lions shown by species-specific differences detected across 25 independent microsatellite loci further support an independent evolutionary history as distinct species (see Fig. 23.4; Wolf et al. 2007). Moreover, sea lion populations found in the most western part of the archipelago on south-west Isabela and Fernandina differ significantly in ecological, morphological and genetic terms with populations found in the remaining part of the archipelago. Foraging mode of sea lions in the central part follows a pelagic shelf feeding, whereas foraging in the deep and nutrient-rich marine habitat in the west requires a completely different foraging mode associated with specific morphological and physiological adaptations. Foraging in the deep and nutrient-rich habitat in the west might be a consequence of inter-specific resource competition with sympatric Galápagos fur seals (*Arctocephalus galapagoensis*) that exploit the deeper zones in the areas where both species overlap. Observed differences of the morphology of the feeding apparatus as well as significant genetic

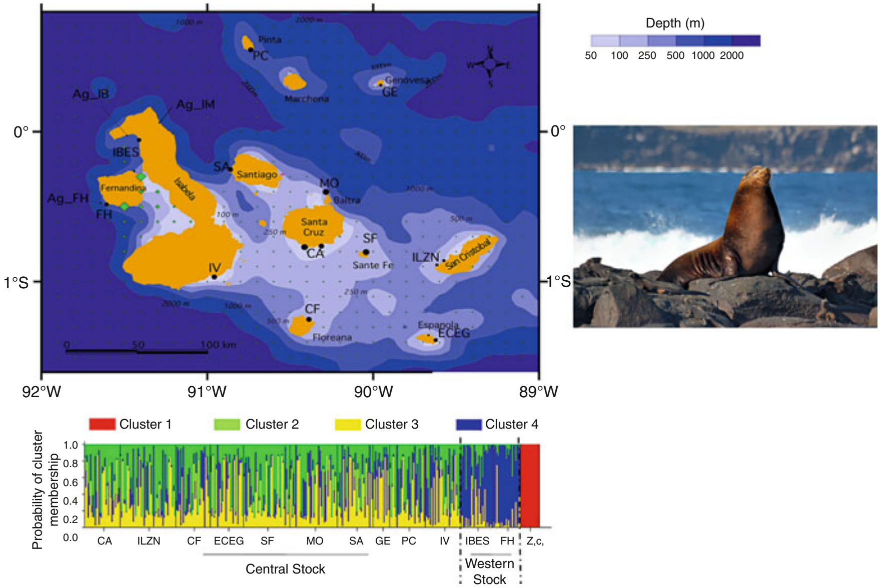

Fig. 23.4 Diversity and distribution of Galápagos sea lions (*Zalophus wollebaeki*) across the archipelago. Note that Galápagos sea lions (*Zalophus wollebaeki*; represented by cluster 2, 3 and 4 in the Bayesian cluster analysis of individual microsatellite genotypes in the lower part of the figure) are quite distinct from the Californian sea lions (*Zalophus californianus*; cluster 1 in the lower part of the figure). Within the archipelago central populations (represented by cluster 2 and 3) are genetically distinct from western populations (cluster 4) that adapted to different ecological conditions due to interspecific competition with syntopic Galápagos fur seals (*Arctocephalus galapagoensis*; indicated by the prefix *Ag*) and different environmental conditions (diamonds symbolize the average chlorophyll a concentration from 1998–2007 indicative for the nutrient level of a given location (from Wolf et al. 2008)

differentiation on the level of microsatellite loci might be indicative of an ecologically driven ongoing speciation process at an early stage (see Wolf et al. 2008).

23.4.4 Land and Marine Iguanas

Terrestrial and marine iguanas are the most striking examples of reptile species endemism and for adaptive evolution of a single lineage to the terrestrial and marine environment on a macroevolutionary scale. Both lineages of iguanas form a monophyletic group within the Iguanidae and are considered sister species that have separated from their ancestors on the Middle American mainland. Based on molecular dating, the divergence of lineages separating marine from terrestrial iguanas must have occurred at least ten million years ago on nowadays already sunken islands of the Galápagos (see also Sect. 23.1). Descendents of both lineages have adapted to completely different environments during their evolution on the archipelago. Marine iguanas exhibit a unique natural history among lizards worldwide, feeding almost exclusively on specific algae species in the intertidal or subtidal zones of larger and smaller islands of the archipelago, while breeding and nesting completely on land. Physical attributes such as a flattened tail for swimming and long, sharp nails for clinging to rocks in the surf enable them to negotiate the marine environment. In contrast, land iguanas are exclusively terrestrial and feed on the islands vegetation.

Marine iguanas display a large morphological variation between distinct islands as expressed by up to twofold differences in total body length and body weight differences that can differ up to tenfold. Additionally, some of the island populations (e.g. individuals from Floreana and Española) also show differences in coloration with regard to the remaining islands. Based on these differences up to seven distinct subspecies of marine iguanas have been described in the past. However, such a differentiaion of island populations was not mirrored by the study of Rassmann et al. (1997), which found no significant differentiation between island populations on the basis of a fragment of the Cytochrome-B gene and on a restricted number of nuclear-coded microsatellite loci. Accordingly, Rassmann et al. suggested that observed morphogical differences might not express genetic differentiation but should be rather seen as plasticity of morphological traits within a single taxon of marine iguana distributed across different islands. A new comprehensive analysis of the population structure of marine iguanas based on a larger set of molecular markers, however, questions a single taxon status of marine iguanas across the archipelago. The study of Steinfartz et al. (2009) indicates the existence of 20 distinct genetic clusters of marine iguanas on the Galápagos, generally following a one-cluster-per-island pattern. On the easternmost island of San Cristóbal even two well-differentiated genetic clusters exist that might be differentiated even on the species level (see Fig. 23.5).

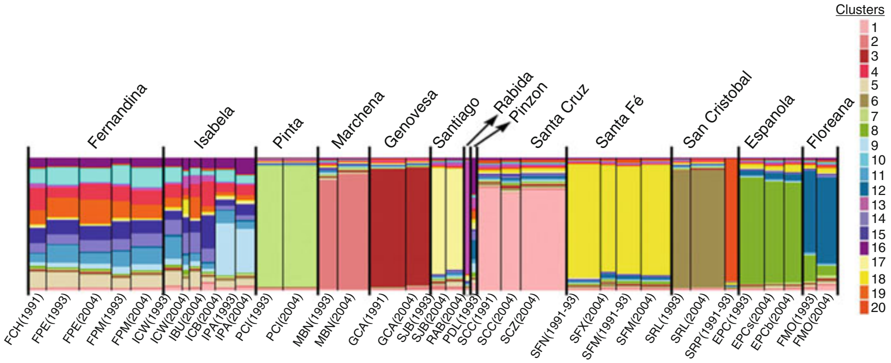

Fig. 23.5 Genetic diversity of Galápagos marine iguanas (*Amblyrhynchus cristatus*). Despite previous views, Galápagos marine iguanas are genetically quite distinct and form up to 20 distinct genetic clusters across the island. Note, that on the island of San Christóbal two very diverse lineages of marine iguanas can be found in the west and east, respectively, that might represent distinct species (from Steinfartz et al. 2009)

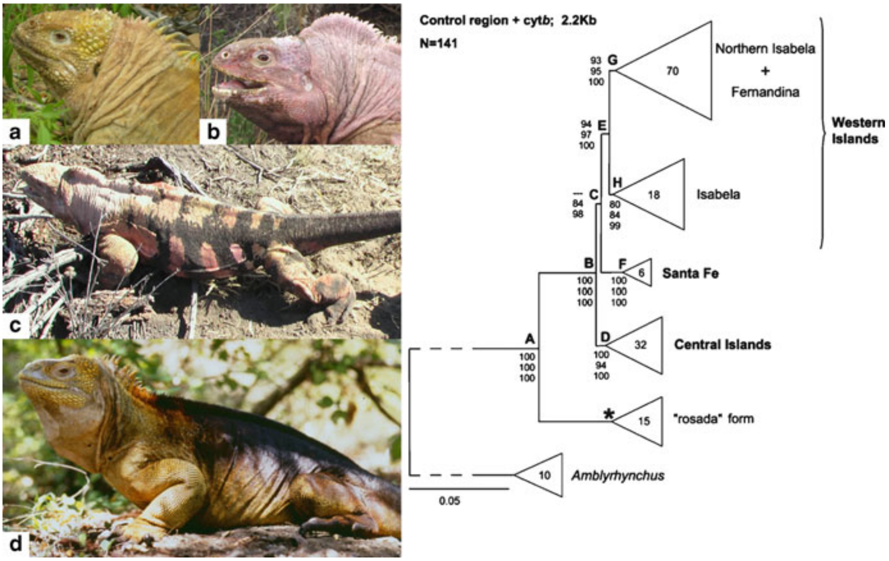

Fig. 23.6 Distinct species of terrestrial iguanas from the Galápagos. *Conolophus subcristatus* from Sierra Negra (**a**) and volcan Wolf (**d**) from Isabela and the newly discovered *Conolophus marthae* (**b** and **c**) also from volcan Wolf. On the *right*, phylogenetic relations of mitochondrial lineages of terrestrial iguanas. Note, that the pink *Conolophus marthae* builds the most basal lineage when rooted with next closely related marine iguanas (*Amblyrhynchus cristatus*) (from Gentile et al. 2009)

Until very recently remnant land iguana populations on the Galápagos were considered to form two distinct species: *Conolophus subcristatus* as found on Santa Cruz and adjacent islets Seymour Norte and Baltra, Isabela and Fernandina and *Conolophus pallidus* as exclusively found on the island of Santa Fé. In 2009, Gentile et al. described the discovery of a so far overlooked species of land iguana (*Conolophus marthae*) from volcano Wolf from northern Isabela (see Fig. 23.6). The pink coloration of this new species differs not only strongly from syntopic yellow *C. subcristatus*; also from a genetic point of view it is highly differentiated and distinct by forming the most basal lineage within the clade of terrestrial Galápagos iguanas.

The discovery of a new species of land iguanas as well as the vast underestimation of genetic distinctness of marine iguana populations that might be comprised in some cases of distinct species reveals that the real extent of species diversity – even for large organisms such as iguanas on the Galápagos – might not be sufficiently explored.

23.5 Threats to Species Endemism of the Galápagos

There are two major sources of threats to the fauna and flora of the Galápagos islands: human-induced changes as well as disturbances (including introductions of alien species) and climatic oscillations, specifically the so-called El Niño event.

Rather soon after its discovery pirates had started at the end of the seventeenth century to exploit giant tortoises because of their meat. Whalers followed the pirates during the eighteenth and nineteenth century and many as 200,000 tortoises have been protracted from the islands as a kind of living tinned food on ships during the nineteenth century. Another dimension of human-induced disturbances on the Galápagos is either actively or passively introduced alien species to the Galápagos. Although not all the introduced species pose the same level of risk to the native flora and fauna, they either predate on or compete with endemic species and are potential hosts or carriers for foreign diseases and parasites, which may have devastating effects on endemic species of the archipelago. Including humans, approximately 23 vertebrate species have been introduced reaching from rats, cats and goats to the arrival of the tree frog *Scinax quinquefasciata* during the wet El Niño period of 1997/1998. On the basis of an extensive plant inventory of the Galápagos islands introduced and alien plants now outnumber native plants by more than one and a half (Guézou et al. 2010).

Domestic goats that are hardy, extremely adaptable and reproduce rapidly have started to invade the archipelago 200 years ago and their numbers soon increased with a devastating effect on the ecosystem of the islands. On Isabela, goats outnumbered tortoises by 20:1 at the beginning of the 1990s. Due to their intense grazing, the original habitat of the island that sustained the largest remnant tortoise populations, became denuded at the expense of starving and outcompeting tortoises that could not graze or find water anymore. At this time cost and man power demanding eradication programs were launched that successfully eradicated goats on most of the islands and natural conditions could rebound rather quickly with a positive effect on the endemic fauna such as populations of giant tortoises on Isabela or rails on Santiago could recover (Campbell 2009). Also, feral dogs that decimated by preying a broad range of endemic species including reptiles (e.g. land and marine iguanas), birds (e.g. penguins) as well as sea lions and fur seals on Isabela have been successfully eradicated from that island.

Along with the active or passive introduction of species or together with contaminated equipment, clothing, or agricultural products possible infectious diseases and pathogens are transported to the Galápagos. While the alien host species are normally well adapted to their pathogens, the immunological system of most of the endemic species had so far no opportunity to build up any resistances against such pathogens or infections. Accordingly, high morbidity and mortality, reduced productivity, and subsequent population decline or extinction of endemic Galápagos species could be the case. Introduced avian malaria, as transmitted by *Plasmodium relictum*, and avian pox virus were the main cause for the extinction of half of the endemic Hawaiian honeycreepers species within the last 200 years. Although until today no bird species of the Galápagos has been lost, this might change in the near future. Pox-like symptoms are already present in Galápagos domestic chickens and wild bird populations and the mosquito species *Culex quinquefascitus*, an important vector of the avian malaria parasite *P. relictum*, has become established on the Galápagos (Parker 2009).

Currently, three different management strategies are followed on the Galápagos to counteract invasive species and introduced infections (1) prevention of the introduction of new species, (2) eradication of introduced species that became invasive and (3) control programs that monitor the presence of possible introduced pathogens and the degree of infections among populations.

Besides human-induced threats, the other main threat to species diversity on the Galápagos – natural driven, but maybe indirectly anthropogenic enforced – is the El Niño warming that is part of the regularly recurring El Niño-Southern Oscillation (ENSO) affecting also the Galápagos archipelago to various degrees. During intense El Niño warming periods, an absence of ocean upwelling causes low food supply and consequently the starvation of many marine organisms. During the most recent, severe El Niños, population crashes of 77% (1982–1983) and 65% (1997–1998) were recorded in the endemic Galápagos penguin, while nearly 100% of Galápagos fur seal yearlings and large males perished. For both, the Galápagos penguins and the Galápagos sea lions repeated El Niño warming might represent nowadays the biggest threat. Also, Galápagos marine iguanas experienced mortality rates as high as 90% on some of the islands. Although a comprehensive genetic study comparing the genetic composition of marine iguana populations before and after the severe El Niño warming of 1997/1998 showed for the majority of island populations no signs of an induced genetic bottleneck, two islands (Genovesa and Marchena) did show clear signs for such an effect (see Steinfartz et al. 2007).

Although paleoclimate data depict a 15,000-year history of El Niño, thus making it part of the natural evolutionary processes acting on species such as sea lions, penguins and marine iguanas on the Galápagos, climate models suggest that the strength and frequency of El Niño events have recently increased, and will continue to do so, due to global warming. So far marine species, which are negatively affected by El Niño events, seem to have managed to survive the impacts of this natural force as population size could always rebound during less intense El Niño events. However, more frequent and severe El Niño events in combination with other selective forces (e.g. introduced pathogens or natural catastrophes) could drive populations – as indicated for marine iguanas on Marchena – to the edge of extinction. Once population size has decreased, as is the case for the Galápagos penguins and a clear tendency is seen also for Galápagos sea lions, that are presently estimated as half as large as they were 30 years ago (Trillmich 2009), El Niño events will turn from an evolutionary-balanced force into a possibly extinctive one.

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Part V
Marine Biodiversity

Chapter 24
Hotspots on Global Coral Reefs

Marjorie L. Reaka and Sara A. Lombardi

Abstract Coral reefs represent the pinnacle of marine diversity, but are seriously threatened by human activities. Coral reefs reach highest diversity in the Indo-Australian archipelago, with secondary peaks in the southwestern Indian Ocean and West Atlantic. Diversity declines into the Central Pacific, is lower in the East Pacific than in the Caribbean for most (not all) taxa, and is lowest in the East Atlantic. Endemism varies with scale – local endemism shows no significant geographic pattern, but regional endemism is high in the Indo-Australian archipelago, moderate in the western Indian Ocean and Central Pacific, and highest in the Americas, especially the East Pacific. Among all studies, species diversity correlates significantly with average threat (local impacts, ocean warming and acidification, bleaching, disease, inadequate protection), but neither local nor regional endemism correlates with threat or diversity. When diversity, endemism, and threat are combined to form local hotspots, Indonesia, the Philippines, New Caledonia, the islands of southern Japan, and southeastern Africa merit highest conservation attention. Regionally, especially the Indo-Australian archipelago, but also the East Pacific, the Caribbean, greater Australia, and the western Indian Ocean deserve highest current conservation priority. However, projected mega-scale environmental changes such as ocean warming and acidification pose particular challenges and may alter how we set regional priorities in the future. We conclude with a discussion of the controversies surrounding coral reef hotspots and their possible resolution.

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Abbreviations

Terminology for the IAA is reviewed in Hoeksema (2007)

AO	Atlantic Ocean
$\Omega_{\text{aragonite}}$	Saturation Level of Aragonite in Sea Water
CAR	Caribbean
CP	Central Pacific
EA	East Atlantic
EP	East Pacific
GBR	Great Barrier Reef
GOM	Gulf of Mexico
IAA	Indo-Australian Archipelago
IO	Indian Ocean
IP	Indo-Pacific
IPCC	Intergovernmental Panel on Climate Change
ISJ	Islands of Southern Japan
ME	Middle East
MPA	Marine Protected Area
PO	Pacific Ocean
SEA	Southeast Asia
SWIO	Southwest Indian Ocean
WA	West Atlantic
WCP	West Central Pacific
WIO	West Indian Ocean
WPM	West Pacific Margin

24.1 Introduction: How Can We Save as Much of Global Coral Reefs as Possible, Given Limited Time and Resources?

The original concept of biodiversity "hotspots" – sites where exceptional concentrations of endemic species are subject to exceptional rates of habitat loss – was motivated by the need to establish conservation priorities in rapidly degrading, usually diverse terrestrial habitats (Myers 1988, 1990, 2003; Myers et al. 2000; Mittermeier et al. 2004). Later additions to the concept include high overall diversity of the site, concentrations of higher taxa, concentrations of rare or threatened species, concentrations of evolutionarily ancient or unique taxa, concentrations of "phylogenetic diversity" (length of evolutionary pathways that connect taxa), potential for future evolutionary novelty, complementarity, and other indicators of vulnerability such as human population growth and climate change. In many studies, endemism is a good surrogate with which to prioritize conservation areas, since, because of their small ranges and extinction vulnerability, more species may be saved if areas characterized by high endemism are targeted than if areas characterized by high species diversity are selected (Williams et al. 1996; Bonn et al. 2002; Orme et al. 2005; Lamoreaux et al. 2006).

Although successful in focusing conservation efforts and galvanizing support for conservation over the last 20 years, the hotspot approach has been controversial because centers of endemism (a) are not always congruent among different taxa; (b) may not coincide with areas of high overall diversity or threat; (c) may miss rare or threatened species in other (especially non-tropical) regions; (d) may not protect megafauna (especially top carnivores) with large geographic ranges; (e) may fail to include lineages with unique evolutionary adaptations for particular habitats; and (f) may fail to protect landscapes that are spectacular or culturally important to humans. Myers (2003), Mittermeier et al. (2004) and others have addressed these concerns, noting that the urgency is great and that sufficient funds are available to mitigate considerable species loss if prioritized and wisely allocated.

Other recent work has re-emphasized the value of conservation area prioritization, with the goals of ensuring that biodiversity is adequately represented, and will persist, in place-based conservation sites and networks (Pressey et al. 1993; Wood 2007; Wood and Dragicevic 2007; Langhammer et al. 2007; Illoldi-Rangel et al. 2008 and others). Like the hotspot approach, these efforts usually depend on species (in the context of a functioning ecosystem) as the relevant unit of biodiversity, place a fundamental value on conserving the maximal number of species, and focus especially on the architectures of threats and protected areas. Such studies often use a hierarchical system of objectives that span different temporal and spatial scales and address socio-political as well as biodiversity issues. Reviewing the concepts and methods behind conservation prioritization, Brooks et al. (2006) identify nine major approaches that all fit within a framework of “irreplaceability” vs. “vulnerability.” A common measure of irreplaceability is endemism (but other aspects of irreplaceability include phylogenetic uniqueness, unusualness, or global rarity of a major habitat type). Vulnerability can include rate of habitat loss, amount of protected area coverage, or human population characteristics. Thus, the hotspot tradition leaves a strong imprint on the ongoing work of identifying and prioritizing areas of conservation need in an era of accelerating human impact, limited time, and, often, scarce resources.

For marine organisms, central questions in the debate about how to identify priorities for conservation include: How much should we rely on the distribution of total species diversity (often the most available data) vs. concentrations of endemic species (data often unavailable or inconsistent among studies), how do diversity and endemism overlap with the distribution of threat and protection, and at what scales should these characteristics be considered? Scale is important for both conservation planning (Erasmus et al. 1999; Hughes et al. 2005; Hurlbert and Jetz 2007) and understanding patterns of biodiversity (Bellwood and Hughes 2001; Mora et al. 2003; Reaka et al. 2008). For example, our studies (Reaka et al. 2008 and below) show that centers of endemism are not evident at local or subregional scales but significant patterns of endemism can be seen at regional scales – this likely explains why some studies fail to find congruence between endemism and threat, endemism and species diversity, or patterns of endemism among different taxa. Furthermore, different measures of biodiversity, such as alpha (local site), beta (species turnover or between-habitat) and gamma (regional) diversity, can produce different results – resulting in different levels of hotspot designation – even within one area (Price 2002).

This paper will focus on how species diversity, endemism, different types of threats, and protection are distributed on global coral reefs, and will employ a normalized ranking procedure incorporating all of these characteristics to identify the most important local and regional coral reef hotspots on a global basis. We will also discuss the controversies surrounding hotspots on coral reefs and their possible resolution.

24.2 Hotspots of Diversity, Endemism, and Threat on Global Coral Reefs

24.2.1 The Geography of Species Diversity on Global Coral Reefs

Although it has long been recognized that coral reefs reach pinnacles of diversity (used equivalently with species richness here) in the Indo-Pacific (IP, see Abbreviations) and WA, plotting patterns of species diversity from various coral reef taxa reveals a strikingly consistent "bulls-eye" pattern (Bellwood and Meyer 2009) of richness in the IAA. Drawn from various studies on patterns of species diversity, Fig. 24.1 presents composite contours of diversity for fishes, gastropods, stomatopods, lobsters, corals, and benthic reef algae not previously assembled. Similar patterns are found in non-reef tropical assemblages such as sea grasses and mangroves (Groombridge and Jenkins 2002; Spalding et al. 2003; Hoeksema 2007).

The highest peak of current global coral reef biodiversity, by far, occurs in the IAA. Diversity slopes to the east on the WPM and reaches another peak in the SWIO, approximating levels in the WPM. In algae, high diversity occurs further north on the African coast than the SWIO center observed in other taxa. CAR/Antillean diversity approximates that of the WIO/SWIO and the WPM in fishes, stomatopods, lobsters, and algae. However, WA diversity in gastropods and corals is lower than that in the WIO, only approximating that of the CP. According to the six broad categories of species richness applied to each taxon, EP diversity is lower than CAR/Antillean diversity in fishes, stomatopods, lobsters, and algae (but not gastropods and corals). In gastropods, a pocket of EP diversity exceeds that in the WA, and stomatopod species richness is moderately high in the EP (though lower than in the WA), being comparable to that of the WPM, WIO and GOM. All taxa show relatively low diversity in the EA.

These patterns of diversity are quantified in Table 24.1. Indonesia and the Philippines, New Guinea, New Caledonia, the ISJ, and the GBR form the first tier, while western Australia, the Mascarene Islands, South India, the southeastern

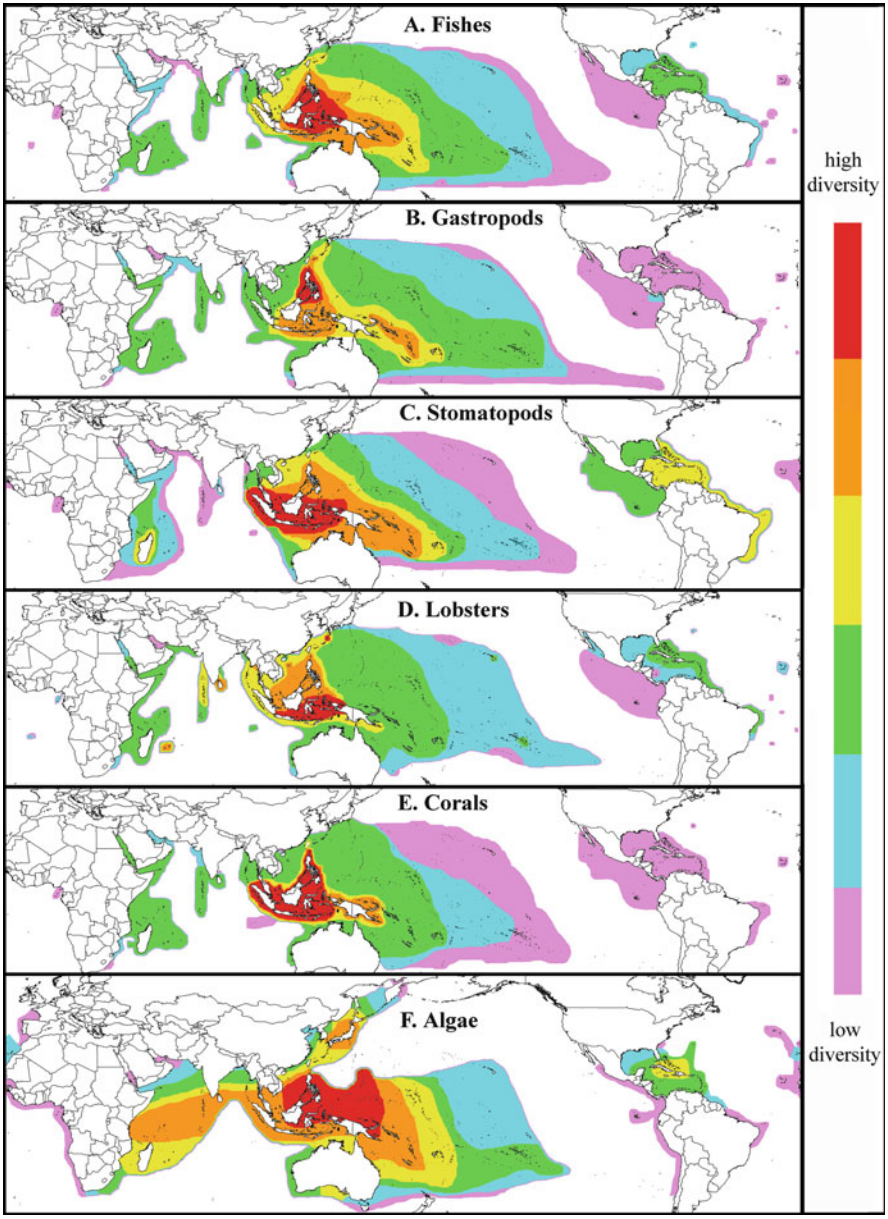

Fig. 24.1 The distribution of total species diversity for different taxa on global coral reefs, including (**a**) fishes, (**b**) gastropods, (**c**) stomatopods, (**d**) decapod lobsters, (**e**) corals, and (**f**) benthic reef algae. Red is highest and violet is lowest diversity for each taxon. Data are derived from the following sources for (**a**) fishes: Randall (1998), Allen (2000, 2007), Bellwood and Hughes (2001), Hughes et al. (2002, 2003, 2005), Roberts et al. (2002), Mora et al. (2003), Bellwood et al. (2005), Bellwood and Meyer (2009); (**b**) gastropods: Briggs (1999), Roberts et al. (2002), Meyer (2003), Meyer et al. (2005), Paulay and Meyer (2006), Hoeksema (2007),

coast of Africa, and the Greater Antilles form a second group of species-rich local sites. Among major regions quantified here, the IAA, the WPM, greater Australia, the WIO, the IO, and the CAR, respectively, are the most diverse.

24.2.2 The Geography of Endemism on Global Coral Reefs

When examined on a local scale, spots of endemism are widespread throughout the IP (Fig. 24.2a, b). Using a metric that combines range rarity in four coral reef taxa (fishes, gastropods, lobsters, and corals), Roberts et al. (2002) identify 18 local centers of endemism that occur both in the IAA and in isolated peripheral areas, although species richness among these taxa peaks in the IAA. Of their five most highly ranked sites for endemism (the ISJ, western Australia, the Gulf of Guinea, the GBR, and the Hawaiian Islands, respectively), three could be considered to fall within the broadly defined IAA (Fig. 24.2b). In addition, their study shows other significant (but lower ranked) sites of endemism in the greater IAA (New Caledonia, Philippines, Sunda Islands). Nevertheless, 12 of their 18 centers of endemism occur in more peripheral areas. To test whether local endemism is associated with species richness in their study, we analyzed numbers of endemic vs. nonendemic species of their combined taxa among the 18 local sites of high endemism to determine if more endemics were found in certain locations than would be expected based on the diversity of the location; however, there is no significant association between number of endemics and number of total species among local sites ($p > 0.05$, Spearman rank correlation).

In IP reef fishes, locally endemic species are considered by many authors to be especially concentrated in peripheral or isolated areas, but there is substantial evidence of high endemism in the broadly defined IAA as well. For example, Randall (1998) finds particularly high endemism in Hawaii and Easter Island, and substantial endemism in the Marquesas, Red Sea and SWIO (Fig. 24.2a). Allen (2000, 2007) reports especially high endemism in the Hawaiian Islands and Red Sea, with a second tier of local endemics in the GBR, ISJ, Mascarene Islands, Marquesas Islands, and Oman (Fig. 24.2a). However, when numbers of endemic fish species in selected indicator groups are collated, three sites in the greater IAA

Fig. 24.1 (continued) Bellwood and Meyer (2009); (**c**) stomatopods: Manning (1969, 1995); Reaka and Manning (1987); Reaka et al. (2008, 2009a, b, unpublished data); (**d**) lobsters: Roberts et al. (2002); (**e**) corals: Veron (1995, 2000), Spalding et al. (2001), Bellwood and Hughes 2001; Groombridge and Jenkins (2002), Hughes et al. (2002, 2003, 2005), Roberts et al. (2002), Bellwood et al. (2005), Hoeksema (2007); (**f**) Bryopsidales algae: Kerswell (2006). Details may differ from those of particular studies due to the composite nature of the graphs, which are synthesized across studies; digitized data are not yet widely available for compiling geographic information on diversity among taxa and studies. Some comparisons may be affected by where the number of species in a particular taxon and region fall relative to the breaks between the six categories of diversity we used

Table 24.1 Raw ranking scores (not normalized to mean) for species diversity, endemism, and different types of risk

Locality	Rank for species richness	Rank for endemism	Average rank for threat	Rank for local threats	Rank for temperature	Rank for bleaching	Rank for disease	Rank for ocean acidification	Rank for lack of protection
(a) *Local analyses*									
ISJ	3.3	3.2	1.5	1.8	2.3	1.0	1.0	2.0	1.0
Indonesia and Philippines	1.2	4.0	1.4	1.0	1.0	1.5	1.0	3.0	1.0
New Guinea	2.1	6.5	1.8	1.0	2.0	2.0	2.0	2.8	1.0
New Caledonia	3.2	2.0	2.3	2.0	2.0	4.0	1.0	2.5	2.0
Lord Howe and Norfolk Islands	5.1	8.3	3.5	4.0	4.0	4.0	4.0	1.0	4.0
GBR	3.6	4.6	2.4	4.0	2.6	1.0	1.0	2.0	4.0
Western Australia	3.7	2.8	3.0	4.0	3.0	2.0	3.0	2.0	4.0
Christmas Island	4.8	7.0	2.3	4.0	2.0	1.0	1.0	3.0	3.0
South India	3.8	2.5	2.1	1.0	2.0	1.0	2.0	3.5	3.0
Oman	4.8	7.2	2.8	4.0	1.5	2.0	4.0	2.0	3.0
Red Sea	5.0	2.4	2.2	2.0	3.0	2.0	1.0	–	3.0
Southeast African Coast	4.2	2.5	1.9	1.8	2.7	1.0	1.8	2.0	2.0
Mascarene Islands to Eastern Madagascar	3.7	7.0	2.4	1.2	3.0	4.0	1.0	3.0	2.5
Gulf of Guinea	5.8	2.0	2.8	1.0	2.0	4.0	4.0	3.0	3.0
Greater Antilles	4.3	2.5	1.8	1.0	2.5	1.0	1.0	3.5	2.0
Galapagos, Clipperton, Cocos, and Malpelo Islands	5.7	4.4	2.7	4.0	2.0	4.0	3.0	1.0	2.5
Baja California	5.4	2.0	3.2	4.0	4.0	4.0	4.0	1.0	2.0
Easter and Pitcairn Islands	5.8	3.7	2.8	4.0	4.0	1.5	4.0	1.0	2.0
Southeast Polynesia	5.2	5.6	2.8	4.0	3.0	.02	3.0	2.5	2.0
Hawaiian Islands	5.3	2.3	2.2	1.5	4.0	2.0	1.0	2.5	2.5

(continued)

Table 24.1 (continued)

Locality	Rank for species richness	Rank for endemism	Average rank for threat	Rank for local threats	Rank for temperature	Rank for bleaching	Rank for disease	Rank for ocean acidification	Rank for lack of protection
(b) *Regional analyses*									
IAA	1.5	3.0	1.6	1.0	1.5	1.0	1.0	3.5	1.0
Australia	3.7	3.0	2.6	3.0	2.3	2.0	2.0	2.0	4.0
Middle East	4.8	4.0	2.0	1.9	2.2	1.5	1.0	2.5	3.0
WIO	3.9	4.0	2.0	1.7	2.2	1.1	2.0	2.5	2.0
IO	4.0	8.5	2.2	3.0	2.1	1.1	1.0	3.0	3.0
Greater CP	5.0	6.4	2.7	2.8	2.8	2.0	3.0	3.5	2.0
WPM	3.5	10.0	2.3	2.8	2.1	2.0	2.0	2.9	2.0
EP	5.6	1.0	1.4	1.5	2.0	1.0	1.0	1.0	2.0
CAR	4.5	2.0	1.8	1.1	2.2	1.0	1.0	3.7	2.0
GOM	5.2	11.0	2.6	3.0	3.0	3.0	2.0	2.9	2.0
Brazil/AO	5.6	2.0	2.6	1.9	3.0	2.0	2.0	3.8	3.0
EA	5.8	3.0	2.9	1.0	2.5	4.0	4.0	2.8	3.0

At each locality, rank for species diversity is derived from Fig. 24.1 for each taxon, and then the ranks of all six taxa are averaged (1 = highest diversity) for that locality. Ranks for local and regional endemism are from Table 24.3 and Fig. 24.2a, b (1 = highest endemism). Ranks for local anthropogenic threats, temperature stress, bleaching, and disease are derived from Figs. 24.2c, d and 24.3 (1 = highest threat). For local anthropogenic threats, bleaching, and disease, ranks 1 and 2 = high and medium threat due to number and spatial concentration of sites impacted, 3 = some threat but not over most of the area in the site considered, 4 = occurrence not sufficiently severe to appear on this map but not necessarily absent. Even though a small isolated island or island chain (e.g., Easter Island, Chagos Islands) may have suffered only one severe bleaching or disease event, it is ranked relatively highly for impact because of small or isolated reef area. Risk due to ocean acidification is ranked according to the contours in Fig. 24.2e, f (1 = highest risk). Risk due to low % of overall coverage by MPAs, low % of reefs with "adequate" or "partial" protection, high % of reefs with "limited" or "very limited" protection, and low % of their protected areas having "adequate" or "partial" protection is derived from Table 24.4 (1 = highest risk). The regional levels of threat due to lack of protection from Table 24.4 are applied to sites in the local analysis here unless a local site has a somewhat effective MPA, in which case the regional risk is reduced by a half rank for that particular site. Abbreviations and definitions of local and regional areas follow those in the text. Regional sites are based on those discussed herein for diversity and endemism but also include those examined for degree of legal protection of reefs by Mora et al. (2006).

(Indonesia, the Philippines and the ISJ) are the first, third and fourth ranked areas throughout the IP for number of local endemics (Allen 2000, 2007). Also, two sites in Indonesia fall in the top ten of all sites in Allen's study when examined for number of endemics/unit area. Hughes et al. (2002) find the highest local endemism for fishes on the southeast coast of Africa and in New Caledonia, with a second tier of very high endemism in southwestern Australia, New Guinea, and Hawaii (Fig. 24.2a). Furthermore, of all localities in their study, Mora et al. (2003) record by far the highest numbers of local endemics in the "Coral Triangle" of the IAA (Indonesia, Philippines, New Guinea; Hoeksema 2007), with the Red Sea and New Caledonia forming a distant second tier, and the GBR, ISJ, and Mascarene Islands forming a third cohort (Fig. 24.2a). The highest numbers of locally endemic species of reef stomatopods also are found in Indonesia (Fig. 24.2a), although, as Reaka et al. (2008, 2009a) point out, more endemics would be expected there by chance because of the diversity peak in that area (Fig. 24.1c). Numbers of neither local nor subregional stomatopod endemics differ from those expected when the diversities of their local and subregional stomatopod faunas are considered. As currently understood taxonomically, corals show almost no local endemism except in the Red Sea and, to a minor extent, Hawaii (Fig. 24.2b; Hughes et al. 2002).

When all sites that rank most highly for endemism among all taxa in the present study are considered (Table 24.2a), the rank for local endemism does not vary significantly between the broadly defined IAA (Indonesia, Philippines, New Caledonia, western Australia, ISJ, GBR, New Guinea) and more peripheral sites (South India, Oman, Red Sea, southeastern African coast, Mascarene Islands, Hawaiian Islands, southeastern Polynesia, Greater Antilles, Gulf of Guinea; $p > 0.05$, Mann Whitney U test). The lack of significant geographic pattern in studies of local endemism may be influenced by different phylogenetic histories, life histories, and ecological characteristics among taxa; by the locations of institutions and study sites of taxonomic specialists in different groups; and by the different methods used to assess and rank endemism among studies. For example, Allen (2000, 2007) reports different results according to whether sites are ranked by absolute number of endemics, percentage endemics or endemics/unit area. Also, different researchers have examined taxa of greater or lesser inclusiveness (examining only certain families or broader taxonomic groups), resulting in different numbers of endemic species reported for particular localities among studies. Furthermore, pattern is reduced by the fact that almost all of these studies focus on endemism at local rather than broader scales.

In contrast to the lack of pattern in endemism observed at local and subregional scales, the number of IP reef stomatopod endemics is significantly different from those expected from total species diversity when examined at the regional scale. In the IWP (Reaka et al. 2008, 2009a), endemism is highest (47.5%) in the IAA, drops significantly in both adjacent oceanic regions (11.5% in the mid-IO and 7.7% in the WPM), but then again rises toward the west on the WIO continental margin (25.9%) and toward the east into the CP (15.0%). Except for the CP, this pattern parallels that seen for diversity (Fig. 24.1c). However, Atlanto-EP regions show higher endemism than anywhere in the IP (88.2, 75.0 and 50.0% in the EP, CAR, and EA, respectively), except for the GOM, where only 5.9% of coral reef stomatopods are endemic (Reaka et al. 2009b, unpublished data).

Endemism in IP reef fishes shows a similar pattern when examined at a broader scale (Allen 2000, 2007; Table 24.2b). Whereas concentrations of locally endemic reef fishes are scattered throughout the IP, regional endemism is highest in the IAA (28.0%), lower in the combined IO continental and oceanic areas (25.9%), and lowest in the combined WCP and CP regions (19.4%, Fig. 24.2b), strongly paralleling the pattern for total fish species diversity in the IP (Fig. 24.1a). As found in stomatopods, however, regional endemism for fishes is higher (86.7%), and diversity lower, in the EP than in the IP.

Therefore, it is of interest to document endemism on a local scale so that the relationship between extinction vulnerability and local anthropogenic threats can be targeted for conservation action. However, to discern patterns and understand the role of endemism in evolutionary dynamics and assembly of species in different communities, it is necessary to view endemism through a broader lens. This has long been recognized by biogeographers, who designate an area as a separate biogeographical province when $\geq$10% of the regional fauna is endemic to that region (Briggs 1995). Patterns of endemism tell us something about the nature of both the environment and evolutionary dynamics, since small geographic ranges can result from either the process of speciation or extinction (Reaka et al. 2008, 2009a; Bellwood and Meyer 2009). In addition, the huge scale of the threats now impinging on coral reefs (global warming, ocean acidification, modification of coastal habitat due to human activities) requires examination of patterns of diversity and endemism at larger scales.

Data for endemism across local and regional scales is given in Table 24.1. Among all studies and taxa, the top local sites for endemism include Baja California, New Caledonia, and the Gulf of Guinea, followed by the Hawaiian Islands and the Red Sea. A third tier of sites includes the Greater Antilles, South India, and southeastern Africa, while western Australia and the ISJ form a fourth cohort. However, several of these areas (Baja California, Gulf of Guinea, Greater Antilles, South India) are provisionally ranked because their rank is derived from a single study and taxon (Table 24.2a). Among global regions, the EP is the premier part of the world for endemism, followed by the WA (CAR, Brazil, AO). The IAA, greater Australia, and EA form a third tier of global regions characterized by high endemism.

24.2.3 The Geography of Risk on Global Coral Reefs

24.2.3.1 Local Anthropogenic Threats

Cognizance of the geographical distribution of threats to coral reefs increased with widespread bleaching and reef degradation in the 1980–1990s, resulting in several intensive mapping efforts that identify areas subject to different levels of

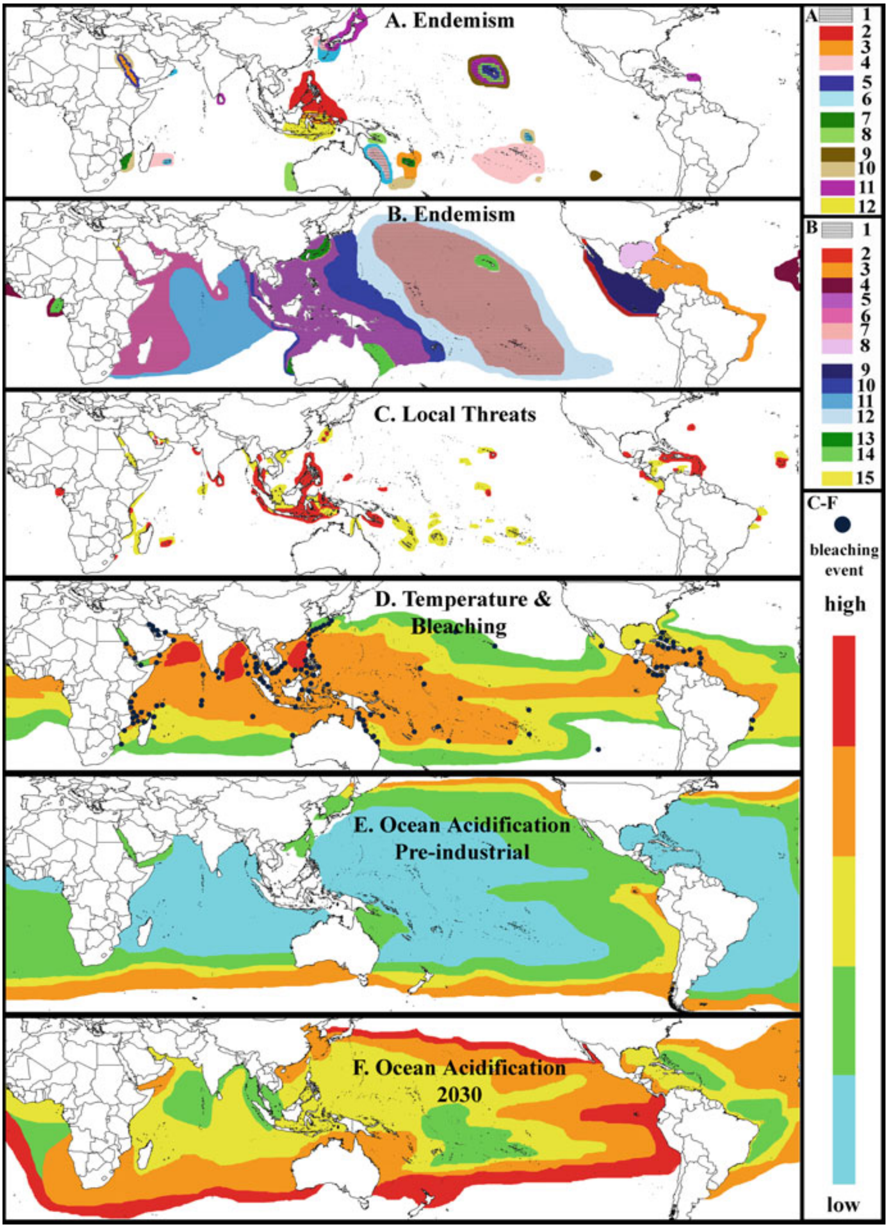

Fig. 24.2 The distribution of endemism (**a**, **b**) and various forms of threats (**c**–**f**) on global coral reefs. In the panels on endemism, **A1**, **B1** = horizontal hatching indicates when the distribution of one taxon overlays another. Gradations within grouped sets of color indicate descending levels of endemism within one study. For reef fishes, **A2** = 90 species are endemic in the IAA, **A3** = 41–43 species are endemic in New Caledonia and the Red Sea, **A4** = 23–33 species are endemic in southeastern Polynesia, the GBR, the ISJ, and the Mascarene Islands (Mora et al. 2003).

anthropogenic impact (Wilkinson 1992, 2008; Bryant et al. 1998; Spalding et al. 2001; Burke et al. 2002; Burke and Maidens 2004). Particularly, the well known *Reefs at Risk* reports by Bryant et al. (1998), Burke et al. (2002), and Burke and Maidens (2004) pinpoint threats to reefs from overfishing and destructive fishing practices, inland land use, coastal development, marine pollution, and synergistic effects of these factors. Further studies have verified that the mere presence of human populations is significantly associated with local degradation of reefs (Green and Bruckner 2000; Sandin et al. 2008).

Combining geographic information from the above authors, Fig. 24.2c summarizes the distribution of reefs at high and medium threat from local anthropogenic factors. As is seen from Figs. 24.1a–f and 24.2a–b, many of the most threatened reef sites have high endemism as well as high total species diversity. The reefs of the IAA and the CAR appear to be at particularly high risk due to local anthropogenic stressors. In comparison, despite its moderately high species diversity and high endemism in some taxa, the SWIO does not have extremely high

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Fig. 24.2 (continued) A5 = 49–63 species are endemic in Hawaii and the Red Sea, and **A6** = 13–26 species are endemic in the Marquesas, GBR, ISJ, Oman, and Mascarene Islands (Allen 2000, 2007). **A7** = 39–42 species are endemic in New Caledonia and southeastern Africa, and **A8** = 26–33 species are endemic in the Marquesas, Hawaii, southeastern New Guinea, western and southwestern Australia (Hughes et al. 2002). **A9** = 22.2–23.1% of species are endemic to Easter Island and the Hawaiian Islands, and **A10** = 4.6–13.7% are endemic to the Marquesas, Australs, Lord Howe/Norfolk, Red Sea, and southeastern Africa (Randall 1998). For benthic reef algae (Kerswell 2006), **A11** = highest number of endemic species=6 (Greater Antilles, Hawaii, ISJ, southern India). In reef stomatopods, **B2** = 88.2% of species are endemic in the EP, **B3** = 75.0% in the WA, **B4** = 50.0% in the EA, **B5** = 47.5% in the IAA, **B6** = 25.9% in the WIO, **B7** = 24.0% in the CP+WCP, and **B8** = 5.8% in the Gulf of Mexico (Manning 1969, 1995; Reaka and Manning 1987; Reaka et al. 2008, 2009a, b, unpublished data). For reef fishes, **B9** = 86.7% of species are endemic in the EP, **B10** = 28.0% in the IAA, **B11** = 25.9% in the WIO+IO, and **B12** = 19.4% in the CP+WCP (Allen 2000, 2007). For combined fishes, gastropods, lobsters, and corals, **B13** = 56–75 species are endemic in the ISJ and western Australia, and **B14** = 35–45 species are endemic in the Hawaiian Islands, GBR, and EA (Roberts et al. 2002). In corals, **B15** = 29 species are endemic in the Red Sea (Hughes et al. 2002). In the panels on threats (**c**–**f**), red signifies highest risk, yellow medium risk and blue lowest risk. (**c**) Local anthropogenic threats are derived from Wilkinson (1992, 2008), Bryant et al. (1998), Spalding et al. (2001), Burke et al. (2002), and Burke and Maidens (2004), and include overfishing and destructive fishing, inland land use practices, coastal development, marine pollution, and synergistic impacts of these factors; only high and medium risk are mapped here. (**d**) Contours for thermal stress are derived from the U.S. National Oceanic and Atmospheric Administration's sea surface temperature records from March to May 2010 (Reefbase 2010a); red = 32–34°C, orange = 28–32°C, yellow = 24–28°C, green = 18–24°C. Black dots represent areas of highest intensity bleaching recorded from 1980–2010 (Reefbase 2010a; also see maps in Bryant et al. 1998; Burke et al. 2002; Burke and Maidens 2004). (**e**, **f**) Comparison of aragonite saturation levels ($\Omega_{\text{aragonite}}$) in ocean water prior to the industrial revolution (**E** = 280 ppm atmospheric CO_2) vs. ~2030 (**F** = projected 450 ppm atmospheric CO_2), with red and orange indicating greatest and great risk, respectively, due to low levels of aragonite saturation; yellow signifying levels ≥ the minimum aragonite concentrations necessary for reef growth today ($\Omega_{\text{aragonite}}$ 3.25); and green and blue indicating lesser and low risk, respectively (contours constructed from information in Kleypas et al. 1999a, b, 2001, 2006; Hoegh-Guldberg et al. 2007) numbers of highly threatened sites from the above factors; however, reefs at medium risk are widespread there, and coral bleaching and disease are common in that region.

Quantification of these local anthropogenic threats (Table 24.1) reveals that the Greater Antilles, Indonesia and the Philippines, New Guinea, South India, and the Gulf of Guinea form a first tier of most endangered local sites, with the Mascarene Islands, Hawaiian Islands, ISJ, southeastern Africa, New Caledonia, and Red Sea forming a second group of heavily impacted sites. Among regions, the IAA and EA, followed by the CAR, EP, and WIO are most threatened by local human activities. These indices of local anthropogenic impact, though, do not incorporate the risk of larger scale threats such as ocean warming (with associated bleaching and disease) or ocean acidification.

24.2.3.2 Ocean Warming

Surface ocean temperatures have risen 0.7°C over the last 136 years (Hoegh-Guldberg et al. 2007; Lyman et al. 2010). These studies show that current temperatures – warmer than any that corals have experienced over the last 420,000 years – are projected to increase 1.8–3.4°C by 2100. Moreover, the *rate* of global temperature change over the last century is 2–3 orders of magnitude greater than any over the last 420,000 years (Hoegh-Guldberg et al. 2007). Especially if warm water incursions are extreme, prolonged, or repeated, thermal stress causes corals to bleach (lose their symbiotic algae), resulting in reduced growth and reproduction, elevated susceptibility to disease, increased coral mortality, and longer term declines in topographic complexity that affect diversity and fisheries (Jokiel and Coles 1990; Glynn 1993; Brown 1997; Harvell et al. 2007; Jones et al. 2004; Muller et al. 2008; Pratchett et al. 2008; Weil et al. 2009). Although some authors suggest that corals might be able to migrate or adapt (Ware et al. 1996; Buddemeier and Smith 1999), numerous studies conclude that, if current rates of warming persist, coral reefs may suffer enormous losses (Hoegh-Guldberg 1999; Donner et al. 2005; Hoegh-Guldberg et al. 2007).

Figure 24.2d shows current temperature contours spanning the global distribution of reefs (Reefbase 2010a). These contours are dynamic, capable of enlarging and intensifying during seasonal, annual, or decadal variations such as those associated with El Niño-Southern Oscillation events. The red and orange contours (28–34°C) are near the upper thermal tolerances for corals (32–34°C, Coles et al. 1976). Although some relatively restricted areas (red = 32–34°C) of the Arabian Sea, Bay of Bengal, and East China Sea approach lethal limits for corals now, their proximity to the species-rich Malay Peninsula, Indonesia, New Guinea, the Philippines and the ISJ poses a serious danger if these thermal areas enlarge. The orange regions (28–32°C) represent a threat to most of the world's coral reefs should they expand or increase in temperature.

Quantification of levels of temperature risk among the local and regional areas examined for diversity and endemism in (Table 24.1) shows that the reefs of

Table 24.2 Comparisons of the number of locally (a) and regionally (b) endemic coral reef species among sites and among studies in descending order (rank 1 = highest endemism)

	Taxon	Number of endemic species	Rank of this site for endemism compared to other sites within each study. Rank of 1 = highest number of endemic species among all sites within that study	Average rank of each site among studies	Reference
(a) *Local analyses*					
New Caledonia	Fishes	39	2 of 43 sites (number)	2	Hughes et al. (2002)
New Caledonia	Fishes	43	2 of 32 sites (number)	2	Mora et al. (2003)
Gulf of Guinea	Combined taxa	45	2 of 18 sites (number)	(2)	Roberts et al. (2002)
Baja California	Fishes	80	2 of 10 sites (%)	(2)	Allen (2000, 2007)
Hawaiian Islands	Combined taxa	35	5 of 18 sites (number)	2.3	Roberts et al. (2002)
Hawaiian Islands	Fishes	49–63	1.5 of 34 sites (categories in figure)	2.3	Allen (2000, 2007)
Hawaiian Islands	Fishes	100	1 of 10 sites (%)	2.3	Allen (2000, 2007)
Hawaiian Islands	Fishes	100	2 of 10 sites (number)	2.3	Allen (2000, 2007)
Hawaiian Islands	Fishes	33	3.5 of 43 sites (number)	2.3	Hughes et al. (2002)
Hawaiian Islands	Fishes	131	1 of 7 sites (%)	2.3	Randall (1998)
Hawaiian Islands	Corals	7	2 of 43 sites, 2 of 2 sites with measurable endemism (number)	2.3	Hughes et al. (2002)
Hawaiian Islands	Benthic algae	6–7	2.5 of 11 sites (number)	2.3	Kerswell (2006)
Red Sea	Fishes	49–63	1.5 of 34 sites (categories in figure)	2.4	Allen (2000, 2007)
Red Sea	Fishes	114	4 of 10 sites (%)	2.4	Allen (2000, 2007)
Red Sea	Fishes	41	3 of 32 sites (number)	2.4	Mora et al. (2003)
Red Sea	Fishes	157	3 of 7 sites (%)	2.4	Randall (1998)
Red Sea	Corals	29	1 of 43 sites, 1 of 2 sites with measurable endemism (number)	2.4	Hughes et al. (2002)
Southeast African coast	Fishes	42	1 of 43 sites (number)	2.5	Hughes et al. (2002)
Southeast African coast	Fishes	–	4 of 7 sites (%)	2.5	Randall (1998)
South India	Benthic algae	6–7	2.5 of 11 sites (number)	(2.5)	Kerswell (2006)
Greater Antilles	Benthic algae	6–7	2.5 of 11 sites (number)	(2.5)	Kerswell (2006)

Western Australia	Combined taxa	56	2 of 18 sites (number)	2.8	Roberts et al. (2002)
Western Australia	Fishes	33	3.5 of 43 sites (number)	2.8	Hughes et al. (2002)
ISJ	Combined taxa	75	1 of 18 sites (number)	3.2	Roberts et al. (2002)
ISJ	Fishes	13–26	4.5 of 34 sites (figure)	3.2	Allen (2000, 2007)
ISJ	Fishes	26	3 of 10 sites (number)	3.2	Allen (2000, 2007)
ISJ	Fishes	31	5.5 of 32 sites (number)	3.2	Mora et al. (2003)
ISJ	Benthic algae	6–7+	2.5 of 11 sites (number)	3.2	Kerswell (2006)
Easter/Pitcairn Is.	Fishes	17	3 of 10 sites (%)	3.7	Allen (2000, 2007)
Easter/Pitcairn Is.	Fishes	–	6 of 10 sites (per area)	3.7	Randall (1998)
Easter/Pitcairn Is.	Fishes	28	2 of 7 sites (%)	3.7	Randall (1998)
Indonesia/Philippines	Fishes	58	1 (Indonesia) of 10 sites (number)	4.0	Allen (2000, 2007)
Indonesia/Philippines	Fishes	–	8, 10 of 10 (Indonesia) sites (per area)	4.0	Allen (2000, 2007)
Indonesia/Philippines	Stomatopods	22	1 (Indonesia) of 21 local sites (%)	4.0	Reaka et al. (2008, 2009a)
Indonesia/Philippines	Fishes	31	3 (Philippines) of 10 sites (number)	4.0	Allen (2000, 2007)
Indonesia/Philippines	Fishes	90	1 (Indonesia and Philippines) of 32 sites (number)	4.0	Mora et al. (2003)
Galapagos, Clipperton, Cocos, Malpelo Is	Fishes	35	6, 7, 8 of 10 sites (%) 1, 2, 3, 4 of 10 sites (per area)	4.4	Allen (2000, 2007)
Australia/GBR	Combined taxa	43	4 of 18 sites (number)	4.6	Roberts et al. (2002)
Australia/GBR	Fishes	13–26	4.5 of 34 sites (categories in figure)	4.6	Allen (2000, 2007)
Australia/GBR	Fishes	22	6 of 10 sites (number)	4.6	Allen (2000, 2007)
Australia/GBR	Fishes	33	4 of 32 sites (number)	4.6	Mora et al. (2003)
Marquesas Islands	Fishes	47	5 of 10 sites (number)	4.9	Allen (2000, 2007)
Marquesas Islands	Fishes	13–26	4.5 of 34 sites (categories in figure)	4.9	Allen (2000, 2007)
Marquesas Islands	Fishes	47	5 of 10 sites (%)	4.9	Allen (2000, 2007)
Marquesas Islands	Fishes	–	5 of 7 sites (%)	4.9	Randall (1998)
Austral Islands (Rapa)	Fishes	–	5 of 10 sites (area)	5.5	Allen (2000, 2007)
Austral Islands (Rapa)	Fishes	14	6 of 7 sites (%)	5.5	Randall (1998)
New Guinea	Fishes	26	5 of 43 sites (number)	6.5	Hughes et al. (2002)
New Guinea	Fishes	12	8 of 10 sites (number)	6.5	Allen (2000, 2007)
Mascarene Is./ E Madgascar	Fishes	13–26	4.5 of 34 sites(categories in figure)	7	Allen (2000, 2007)

(continued)

Table 24.2 (continued)

	Taxon	Number of endemic species	Rank of this site for endemism compared to other sites within each study. Rank of 1 = highest number of endemic species among all sites within that study	Average rank of each site among studies	Reference
Mascarene Is./ E Madgascar	Fishes	42	9 of 10 sites (%)	7	Allen (2000, 2007)
Mascarene Is./ E Madgascar	Fishes	–	7, 9 of 10 sites (per area)	7	Allen (2000, 2007)
Mascarene Is./ E Madgascar	Fishes	31	5.5 of 32 sites (number)	7	Mora et al. (2003)
Southeastern Polynesia	Fishes	23	7 of 32 sites (number)	(7)	Mora et al. (2003)
Christmas Island	Fishes	10	7 of 10 sites (per area)	(7)	Allen (2000, 2007)
Oman	Fishes	13–26	4.5 of 34 sites (categories in figure)	7.2	Allen (2000, 2007)
Oman	Fishes	24	10 of 10 sites (%)	7.2	Allen (2000, 2007)
Oman	Fishes	14	7 of 10 sites (number)	7.2	Allen (2000, 2007)
Lord Howe/Norfolk Is	Combined taxa	31	7 of 18 sites (number)	8.3	Roberts et al. (2002)
Lord Howe/Norfolk Is	Fishes	3–7	10 of 34 sites (categories in figure)	8.3	Allen (2000, 2007)
Lord Howe/Norfolk Is	Fishes	9	15.5 of 43 sites (number)	8.3	Hughes et al. (2002)
Lord Howe/Norfolk Is	Fishes	20	7 of 7 sites (%)	8.3	Randall (1998)
Lord Howe/Norfolk Is	Fishes	43	2 of 32 sites (includes New Caledonia; number)	8.3	Mora et al. (2003)
Mexico	Fishes	11	9 of 10 sites (number)	(9)	Allen (2000, 2007)
(b) *Regional analyses*					
EP	Fishes	127	1 of 4 regions (%)	1	Allen (2000, 2007)
EP	Stomatopods	5	1 of 11 regions (%)	1	Reaka and Manning (1987), Reaka et al. (2008, 2009a), Reaka and Lombardi (2011)
CAR	Stomatopods	18	2 of 11 regions (%)	(2)	Reaka and Manning (1987), Reaka et al. (2008, 2009a), Reaka and Lombardi (2011)

IAA	Fishes	149	2 of 4 regions (%)	3	Allen (2000, 2007)
IAA	Stomatopods	29	4 of 11 regions (%)	3	Reaka and Manning (1987), Reaka et al. (2008, 2009a), Reaka and Lombardi (2011)
EA	Stomatopods	3	3 of 11 regions (%)	(3)	Reaka and Manning (1987), Reaka et al. (2008, 2009a), Reaka and Lombardi (2011)
WIO	Fishes	180	3 (IO/WIO) of 4 regions (%)	4	Allen (2000, 2007)
WIO	Stomatopods	11	5 (WIO) of 11 regions (%)	4	Reaka and Manning (1987), Reaka et al. (2008, 2009a), Reaka and Lombardi (2011)
Greater CP	Fishes	174	4 (CP/WCP) of 4 regions (%)	6.4	Allen (2000, 2007)
Greater CP	Stomatopods	6	6 (CP/WCP) of 11 regions (%)	6.4	Reaka and Manning (1987), Reaka et al. (2008, 2009a), Reaka and Lombardi (2011)
Greater CP	Stomatopods	3	7 (CP) of 11 regions (%)	6.4	Reaka and Manning (1987), Reaka et al. (2008, 2009a), Reaka and Lombardi (2011)

(continued)

Table 24.2 (continued)

	Taxon	Number of endemic species	Rank of this site for endemism compared to other sites within each study. Rank of 1 = highest number of endemic species among all sites within that study	Average rank of each site among studies	Reference
Greater CP	Stomatopods	3	8.5 (WCP) of 11 regions (%)	6.4	Reaka and Manning (1987), Reaka et al. (2008, 2009a), Reaka and Lombardi (2011)
IO	Stomatopods	3	8.5 of 11 regions (%)	(8.5)	Reaka and Manning (1987), Reaka et al. (2008, 2009a), Reaka and Lombardi (2011)
WPM	Stomatopods	3	10 of 11 regions (%)	(10)	Reaka and Manning (1987); Reaka et al. (2008, 2009a), Reaka and Lombardi (2011)
GOM	Stomatopods	1	11 of 11 regions (%)	(11)	Reaka and Manning (1987), Reaka et al. (2008, 2009a), Reaka and Lombardi (2011)

The sites of high endemism were identified by having the greatest numbers of endemic species (or by belonging to sets of sites characterized by the highest numbers of endemic species) within each of the studies. The method used for establishing rank for endemism (number of endemics, % of endemics, endemics per unit area, categories of endemic richness) in each study is given in parentheses. When only one study was available for a site, the rank is included in the column for average rank but enclosed within parentheses to indicate its provisional nature. In Roberts et al.'s (2002) study, "combined taxa" includes fishes, gastropods, lobsters, and corals. Benthic algae are the reef-dwelling Bryopsidales (Kerswell 2006). Geographic abbreviations and definitions follow those in the text

Indonesia, the Philippines, and Oman are at the highest risk of temperature stress. However, the Galapagos and other EP islands, New Caledonia, New Guinea, Christmas Island, southern India, and Gulf of Guinea, followed by the ISJ and Greater Antilles, form second and third tiers of local sites at risk of thermal stress. At the regional level, the IAA, EP, WPM and IO, and then the CAR, ME, and WIO, are most threatened by ocean warming.

24.2.3.3 Coral Bleaching

Intense coral bleaching events (Reefbase 2010a), shown by black dots on Fig. 24.2d, integrate the amount of thermal (and other) stresses that have impacted corals in these localities over the last three decades. Bleaching events are notably concentrated throughout the IAA (especially in the Malay Peninsula, SEA, Philippines, GBR, and ISJ). Severe bleaching also occurs in the SWIO, Persian Gulf, southern Central America, and throughout the CAR (especially the Greater and Lesser Antilles). Except for the Persian Gulf, these regions are associated with both high endemism and high species diversity in most taxa.

Our quantification of the pattern of bleaching (Table 24.1) indicates that, among local sites, the Greater Antilles, ISJ, GBR, Christmas Island, southern India, and southeastern Africa all suffer equally from the most intense bleaching events. Easter Island, Indonesia, and the Philippines form a second tier, and southeastern Polynesia, the Hawaiian Islands, New Guinea, western Australia, Oman, and the Red Sea comprise a third cohort of sites with severe bleaching. Among regions, the CAR, EP, and IAA are most severely impacted by bleaching, with the IO and WIO forming a second group of regions at serious risk.

24.2.3.4 Coral Disease

In addition to bleaching, the frequency and severity of coral diseases has increased in recent decades (Weil et al. 2000; Aronson and Precht 2001; Francini-Filho et al. 2008; Miller et al. 2009; Croquer and Weil 2009). Although most common and severe throughout the CAR and adjacent Pacific Central America, severe coral disease outbreaks occur across the tropical IP as well (Fig. 24.3, Reefbase 2010b). The Red Sea, Persian Gulf, and ISJ are subject to very high levels of disease. Guam and nearby islands, the Philippines, and the GBR have a high incidence of disease, but both sides of Thailand, the Sunda Islands, Fiji and Hawaii also are characterized by concentrated disease outbreaks. Although not as concentrated spatially, some local sites in the SWIO are heavily impacted.

When disease intensity is quantified for the local sites examined here (Table 24.1), the Greater Antilles, the Hawaiian Islands, the ISJ, Indonesia and the Philippines, New Caledonia, the GBR, Christmas Island, the Red Sea, and the Mascarene Islands all rank equally highly, while southeastern Africa is next most

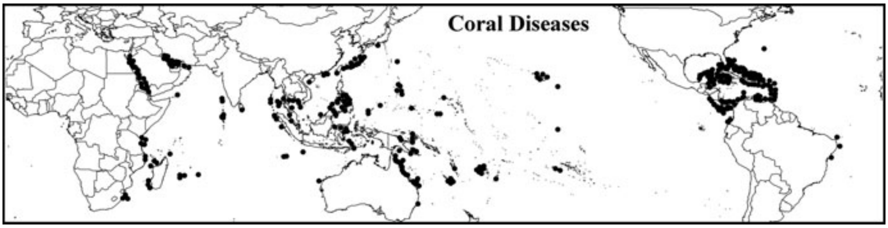

Fig. 24.3 The distribution of severe episodes of coral disease on global coral reefs. Data are derived from disease events recorded between 1970 and 2010 (Reefbase 2010b; also see map in Burke and Maidens 2004)

heavily impacted. Among global regions, the CAR, EP, IAA, IO, and ME are most at risk.

24.2.3.5 Ocean Acidification

The world's atmospheric concentration of CO_2 currently is 390 ppm (IPCC 2010), which is more than 90 ppm above the maximum values that occurred over the last 740,000 and possibly 20 million years (Hoegh-Guldberg et al. 2007). Although there are many uncertainties, the average CO_2 concentration is projected to rise to ~525 (475–550) ppm by the year 2050 and ~800 (650–950) ppm by 2100 (from Fig. 24.1 in IPCC 2010), an increase of ~35% and >100%, respectively, above current levels.

Atmospheric CO_2 diffuses into the ocean and forms dissociated carbonic acid, which lowers the pH of sea water and reduces the ability of sessile and motile organisms to deposit calcium carbonate in their shells and skeletons; specifically, experimental, theoretical, and field studies show that increases in atmospheric CO_2 over the coming century will inhibit aragonite formation, the principal crystalline form of $CaCO_3$ in coral skeleton (Kleypas et al. 1999a, b, 2001, 2006; Orr et al. 2005; Kleypas and Langdon 2006; Hoegh-Guldberg et al. 2007; Fabry et al. 2008). Although average saturation levels were $\Omega_{\text{aragonite}}$ 5.0 (±0.2) in the 1990s, levels are projected to drop to $\Omega_{\text{aragonite}}$ 3.1 (±0.2) by the year 2065 and $\Omega_{\text{aragonite}}$ 2.8 (±0.2) by 2100. Reefs are unable to accrete and erosion accelerates when saturation levels fall below $\Omega_{\text{aragonite}}$ 3.25, which corresponds to atmospheric CO_2 levels of ~480 ppm (Hoegh-Guldberg et al. 2007). These concentrations of atmospheric CO_2 are predicted to occur ~2040 (from Fig. 24.1 in IPCC 2010).

However, pH and $\Omega_{\text{aragonite}}$ are not declining uniformly in the world's oceans. Summarizing information presented in Kleypas et al. (1999a, b, 2001, 2006) and Hoegh-Guldberg et al. (2007), Fig. 24.2e–f compares the geography of $\Omega_{\text{aragonite}}$ in tropical oceans prior to the industrial revolution (280 ppm atmospheric CO_2) vs. ~2,030 (450 ppm atmospheric CO_2, from Fig. 24.1 in IPCC 2010), with red indicating lowest $\Omega_{\text{aragonite}}$ and greatest risk, yellow signifying levels of $\Omega_{\text{aragonite}}$ ~3.25 (the minimum aragonite concentrations associated with coral reefs today), and blue indicating highest $\Omega_{\text{aragonite}}$ and least risk. Whereas almost all coral reefs occurred within either blue or green contours in the pre-industrial era, the projected regions of highly saturated aragonite (blue) are gone and the areas of moderate saturation (green) very reduced by ~2,030. Reefs would still grow well (green) along the Malay Peninsula and Sumatra, the Chagos–Maldive–Lakshadweep archipelagos, a considerable part of the southern CP, the Bahamas and Antilles, and off South America. Minimal reef growth (yellow) still would be possible in the main part of the IAA, much of the WCP, the islands around Madagascar, and much of the CAR and GOM. However, reef growth would be severely compromised (orange) in the ISJ, New Guinea, New Caledonia, Australia, ME, southeastern Africa, and western margin of the WA. Reef sites throughout the EP and the areas stretching eastward from southeastern Australia are in the most serious jeopardy over the next two decades (red).

Quantification of the contours for $\Omega_{\text{aragonite}}$ for the local sites examined here (Table 24.1) shows that Baja California, the Galapagos and other EP islands, Easter and Pitcairn islands, and Lord Howe and Norfolk islands will be most seriously affected by the year 2030. The ISJ, the GBR, western Australia, Oman, and southeastern Africa – followed by southeastern Polynesia and the Hawaiian Islands – form second and third tiers, respectively, of local sites endangered by ocean acidification. Among regions, the entire EP is at highest risk, followed by all of Australia. The ME and WIO form a second tier of regions at near-term risk. However, according to Hoegh-Guldberg et al.'s (2007) calculations, all of the regions in which coral reefs exist today will be devoid of areas with $\Omega_{\text{aragonite}} \geq 3.25$ by the year 2100 (~800 ppm CO_2, IPCC 2010); thus, coral reefs – as we know them today – would be unable to persist.

Manzello et al. (2008) note that EP reefs, which are poorly developed and subject to exceptionally high bioerosion (Eakin 1996; Reaka-Kudla et al. 1996; Glynn 1997), already experience naturally low pH due to upwelling. These authors find low carbonate saturation of sea water and reduced amounts of carbonate cementation on current EP reefs. Whereas dense inorganic cement normally binds reef framework into a coherent whole, poor cementation may facilitate the high levels of bioerosion already observed on EP reefs. Unfortunately, these conditions may portend what will occur on reefs in a high-CO_2 world. The rapid temporal progression and global scope of ocean acidification shown by Kleypas et al. (1999a, b, 2001, 2006) and Hoegh-Guldberg et al. (2007) is cause for grave concern.

24.2.3.6 Inadequate Protection

Bryant et al. (1998), Spalding et al. (2001), Burke et al. (2002), Burke and Maidens (2004), and Mora et al. (2006) map protected areas on global coral reefs. The Papahānaumokuākea Marine National Monument in the Northwest Hawaiian Islands, the GBR, and the Galapagos Islands are the world's three largest coral reef MPAs. Among major world regions, greater Australia has the highest overall MPA coverage (69.7% of reefs with some level of protection, Table 24.3). The EP, CAR, and ME form a distant second cluster (18.1–21.8% of reefs protected). SEA,

Table 24.3 The geography of adequately or inadequately protected regions on global coral reefs, based on information for 980 global MPAs presented by Mora et al. (2006)

Region	% of reefs in each region with some level of protection	% of reefs in each region with "adequate" protection	% of reefs in each region with "partial" protection	% of reefs in each region with "adequate" or "partial" protection	% of reefs in each region with "limited" protection	% of reefs in each region with "very limited" protection	% of *protected* reefs with "adequate" protection	% of *protected* reefs with "adequate" or "partial" protection
Australia	69.7	8.5	60.0	68.5	1.2	0.0	12.2	98.3
ME	18.1	7.7	3.6	11.3	2.9	3.9	42.5	62.4
EP	21.8	3.3	6.2	9.5	8.7	3.6	15.1	43.6
WIO	9.8	2.7	0.9	2.5	1.6	4.6	27.6	36.7
PO	8.3	1.6	1.1	2.7	5.2	0.4	19.3	32.5
IO	2.7	1.5	0.9	2.4	0.3	0.0	55.6	88.9
CAR	20.7	0.7	8.7	9.4	7.3	4.0	3.4	45.4
AO	9.9	0.3	9.3	9.6	0.2	0.1	3.0	97.0
SEA	12.0	0.1	1.1	1.2	1.5	9.3	0.8	10.0
AVERAGE	19.2	2.9	10.2	13.1	3.2	2.9	19.9	57.2

Abbreviations for regions follow those in the text the AO (including Bermuda, Brazil, and EA), WIO, and PO (including the CP and WCP) comprise a third group of regions, with 8.3–12.0% of reefs having some form of legal protection. Only 2.7% of IO reefs are included in MPAs.

However, the effectiveness of protection varies widely (Table 24.3). Only 7.7–8.5% of the reefs in the ME and Australia, 2.7–3.3% of the reefs in the WIO and EP, and 0.1–1.6% of the reefs in SEA, the AO, CAR, IO, and PO are relatively well protected (“adequate” protection, Mora et al. 2006). Australia stands out as having the largest percentage of its reefs with either “adequate” *or* “partial” protection (68.5%); the ME, EP, CAR and AO form the next tier, with ~10% of their reefs having “adequate” *or* “partial” protection. The greater IO, ME, and to a lesser extent the WIO are notable for having relatively high percentages *of their protected areas* effectively managed (55.6, 42.5, and 27.6% of their MPAs with “adequate” protection, respectively). However, Australia, the AO and the IO all have high proportions *of their protected areas* moderately well managed (98.3, 97.0, and 88.9% of their MPAs with “adequate” *or* “partial” protection, respectively). Conversely, even though 12.0% of SEA’s reefs have legal protection status, 9.3% of all SEA reefs have “very limited” protection, only 0.1% of all SEA reefs have “adequate” protection, and few are well managed (only 0.8% *of their protected areas* have “adequate” protection).

When risk due to lack of protection is summarized among the local and regional sites examined here (Table 24.1), the ISJ, Indonesia, the Philippines, and New Guinea comprise the group of local sites in greatest jeopardy. A second tier of local sites threatened by inadequate protection includes the Greater Antilles, Baja California, Easter and Pitcairn islands, southeastern Polynesia, New Caledonia, and southeastern Africa. Among global regions, the IAA is, unsurprisingly, most at risk due to lack of protection. The CAR, GOM, EP, greater CP, WPM, and WIO form a second cohort of regions endangered by inadequate protection.

24.2.4 Global Coral Reef Hotspots: Overlap of Risk, Endemism, and Species Diversity

Table 24.4 summarizes the average normalized rank for all of the above threats to reefs, as well as normalized ranks for endemism and species richness, from all of the local and regional areas considered here. Among all local sites on global coral reefs, the ranks for species diversity are significantly correlated with those for average threat ($p \leq 0.004$, Spearman Rank Correlation), but endemism is not significantly related to either threat or diversity. No significant correlations between diversity, endemism, or threat are detectable among global regions.

Table 24.4a shows that, when the ranks for average threat, endemism and diversity are weighted equally and averaged to provide an index of overall hotspot status for each local site, the coral reefs of Indonesia and the Philippines, New Caledonia, ISJ, Greater Antilles, and southeastern Africa deserve the highest priority for conservation attention. The next tier of local sites that merit priority

Table 24.4 A quantitative summary of hotspot status and its components (species richness, endemism, and threat) for the local (a) and regional (b) sites examined in Reaka and Lombardi (2011)

Rank among sites	Locality	Hotspot status	Rank for species richness	Rank for endemism	Average rank for threat
(a) *Local analyses*					
1	Indonesia and Philippines	**2.2**	1.0	3.5	2.3
2.5	New Caledonia	**2.6**	2.7	1.7	3.5
2.5	ISJ	**2.6**	2.8	2.8	2.2
4.5	Greater Antilles	**2.9**	3.6	2.2	3.0
4.5	Southeast Africa	**2.9**	3.5	2.2	2.9
6	South India	**3.0**	3.2	2.2	3.5
7	Red Sea	**3.2**	4.2	2.1	3.4
9	Hawaiian Islands	**3.4**	4.4	2.0	3.7
9	New Guinea	**3.4**	1.8	5.7	3.0
9	Western Australia	**3.4**	3.1	2.4	4.3
11.5	Baja California	**3.6**	4.5	1.7	4.6
11.5	GBR	**3.6**	3.0	4.0	3.2
13	Gulf of Guinea	**3.8**	4.9	1.7	4.9
14	Easter and Pitcairn Islands	**4.0**	4.9	3.2	3.8
15	Galapagos, Clipperton, Cocos, and Malpelo Islands	**4.1**	4.8	3.8	3.8
16	Southeast Polynesia	**4.3**	4.3	4.9	3.8
17	Mascarene Islands to eastern Madagascar	**4.4**	3.1	6.1	4.1
18	Christmas Island	**4.6**	4.0	6.1	3.0
19	Oman	**4.8**	4.0	6.3	3.8
20	Lord Howe and Norfolk Islands	**5.6**	4.3	7.3	5.2
(b) *Regional analyses*					
1	IAA	**2.1**	1.3	2.4	2.8
2	EP	**2.7**	4.8	0.8	2.4
3	CAR	**2.9**	3.9	1.6	3.2
4.5	Australia	**3.3**	3.2	2.4	4.4
4.5	WIO	**3.3**	3.4	3.2	3.4
6	ME	**3.6**	4.1	3.2	3.5
7	Brazil/AO	**3.9**	4.8	1.6	4.5
8	EA	**4.1**	5.0	2.4	5.0
9.5	Greater CP	**4.7**	4.3	5.1	4.6
9.5	IO	**4.7**	3.5	6.7	3.8
11	WPM	**5.0**	3.0	7.9	4.0
12	GOM	**5.9**	4.5	8.7	4.5

Hotspot status for each locality is the mean rank for diversity, endemism and average threat (the latter is averaged across the six categories of threat discussed in the text. Columns for rank of species richness, endemism and average threat each are adjusted to the same mean for local and for regional analyses, respectively, so that these three components are equally weighted in the column for overall hotspot status. Among local sites (a), species diversity is significantly correlated with average threat ($p < 0.004$, $t = 3.37$, $df = 18$, Spearman Rank, and Pearson's Product–Moment Correlations, data normally distributed), but endemism is not significantly correlated with either average threat or diversity ($p > 0.05$, Spearman and Pearson's Product–Moment Correlations, data normally distributed). Among global regions (b), diversity, endemism, and average threat are not significantly correlated with each other ($p > 0.05$, Spearman and Pearson's Product–Moment Correlations, data normally distributed). Non-normalized data and descriptions of methods used to rank diversity, endemism, and the different forms of threat are available from the authors. Abbreviations and definitions for local and regional sites follow those given in the text conservation action includes southern India, the Red Sea, Hawaiian Islands, New Guinea, and western Australia. If degree of threat is considered the most important factor for prioritization, then especially the ISJ, but also southeastern Africa, New Guinea, Christmas Island, and the GBR should be moved higher. If endemic species are the most important targets of conservation, then particularly the reefs of the Gulf of Guinea and Baja California should be moved to the highest priority alongside those of New Caledonia; in addition, the Hawaiian Islands, Red Sea, Greater Antilles, southeastern Africa, southern India, and western Australia should be moved higher in priority. If species diversity is the most important criterion for conservation, then particularly New Guinea, but also the Mascarene Islands, the GBR, and western Australia should receive higher conservation attention than indicated for hotspots in Table 24.4a.

If diversity, endemism, and the various forms of threat are considered at the regional level, especially the IAA, but also the EP, the CAR, greater Australia, and the WIO should receive highest global conservation priority (Table 24.4b). If degree of threat is the primary consideration for conservation action, the IO should be moved higher than its present rank. If conserving endemics is a primary conservation focus, the reefs of Brazil and the AO should be moved up alongside those of the CAR, just behind the EP. If conservation of species diversity is the main conservation objective, the WPM and IO should be raised to the second tier (after the IAA), and those of the EP and CAR lowered in priority, compared to the ranks they currently occupy. The average overall hotspot status, however, probably represents the most practical way to prioritize conservation efforts for global reefs.

24.3 Discussion

Hotspots on coral reefs have been controversial for some of the same reasons that the approach has been debated in terrestrial systems. Examining the distributions of corals and fishes across the IWP, Hughes et al. (2002) show that centers of high local endemism do not correlate with centers of high diversity, and do not find congruence in patterns of endemism between these taxa (however, this is primarily because corals, as currently understood taxonomically, show little endemism). Examining additional taxa, we also do not detect significant correlations between diversity and endemism or between endemism and threat, but we do find a significant relationship between total species diversity and threat among local (but not regional) sites. Also, although there are minor differences, our analyses show considerable congruence among taxa for patterns of endemism, particularly at larger spatial scales. Differences in patterns of local endemism among taxa and studies likely are due to the scale at which endemism is examined in different studies, methods used to quantify endemism (absolute numbers, % of species, or endemics/unit area) by different researchers, and taxonomic issues.

In one of the most comprehensive studies of hotspots on global reefs, Roberts et al. (2002) examined data for 3,235 species of fishes, corals, snails, and lobsters for patterns of total diversity, endemism, and threat. They report strong concordance among these four taxonomic groups and conclude that areas of endemism are congruent with areas of exacerbated threats to coral reefs. Roberts et al. define endemism as ‘range rarity’ (the reciprocal of range size, where range size is number of 2 × 2° latitudinal × longitudinal cells within the species’ geographic range that contain reef habitat). Their taxa differ in tendency toward range restriction, with lobsters having the smallest and corals the largest ranges. To identify centers of endemism, these authors sum ‘range rarity’ for all species of each taxonomic group within each cell and then map the top-scoring 10% of cells for each taxon onto the global map. Whereas Roberts et al.’s centers of species richness are concentrated in the IAA (Philippines, Indonesia), their centers of local endemism are widely scattered among both isolated peripheral areas and centers of high diversity. Reaka et al. (2008), Bellwood and Meyer (2009), and the present study find the same result.

In response to Roberts et al.’s (2002) paper, Baird et al. (2002) note that many of Roberts et al.’s ‘centers of endemism’ lack endemic corals, which they cite as critical components of reefs. However, in contrast to other taxa, the current taxonomy of corals reveals very little endemism throughout the Pacific (Hughes et al. 2002). In addition, Baird et al. disagree with Roberts et al.’s definition of endemics (the reciprocal of cell number regardless of geographic extent), suggesting that a species may have a broad geographic range encompassing many cells with reef habitat but actually occur in only a few sites. However, Roberts et al.’s approach facilitates comparisons between taxa and studies. Baird et al. also argue that Roberts et al. confound centers of high endemism and high diversity, presumably (although Baird et al. do not discuss this) because centers of endemism result from the summed scores of range-rare taxa (i.e., species-rich areas contain more range rarity scores and thus these sites will be biased toward high numbers of endemic species). However, a number of Roberts et al.’s centers of endemism occur in peripheral areas of low diversity, and our statistical analysis shows no correlation between Roberts et al.’s numbers of local endemics and total species at each site. A solution to this problem would be to use the percentage of species that are endemic in a particular site, as in the original terrestrial literature (e.g., Myers 1988, 1990; Myers et al. 2000) and some reef studies (Randall 1998; Allen 2000, 2007; Reaka et al. 2008, 2009a; Reaka and Lombardi 2011). Many coral reef researchers have tended to use absolute rather than relative numbers of endemics to identify centers of endemism (Table 24.2), but these numbers vary with the taxonomic inclusiveness of the group that is analyzed. Also, different methods of quantifying endemism yield different conclusions about which localities are richest in endemics (Allen 2000, 2007). Another way to identify unusually high levels of endemism is to evaluate significant deviations from a regression line for number of endemics vs. total number of species.

Baird et al. (2002) further criticize Roberts et al. (2002) for focusing on centers of endemism instead of centers of diversity, which Baird et al. view as the “true hotspots” that deserve conservation attention. Briggs (2002) also feels that areas of high total reef diversity are better conservation targets than sites with concentrations of endemic species, noting that endemics often are concentrated in low diversity assemblages on the fringes of the tropics. However, statistical analysis in the present study shows no significant difference in levels of local endemism in central vs. peripheral areas. The present study concurs, though, that total species richness correlates better with degree of threat than does endemism. Nevertheless, the high degree of endemism found in some areas, even peripheral areas of relatively low species diversity, is of fundamental interest because endemics represent species in the process of becoming extinct as well as those in the process of origination (Reaka et al. 2008, 2009a; Bellwood and Meyer 2009). Both of these processes represent critical foci for conservation and maintenance of biodiversity.

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Chapter 25
Biodiversity of a Unique Environment: The Southern Ocean Benthos Shaped and Threatened by Climate Change

Angelika Brandt and Julian Gutt

Abstract Over millions of years, plate tectonics, palaeoceanography and the resulting changes in the global climate (greenhouse to icehouse) have impacted the Southern Ocean marine fauna and flora, caused evolutionary extinctions and radiation of benthic marine invertebrates, and led to the present biodiversity. Simultaneous biogeographical events happening were the progressive retraction of cosmopolitan taxa established during the Jurassic and Cretaceous periods when Antarctica was still under greenhouse conditions. The disjunctive distribution patterns resulted from vicariance due to the disintegration of the supercontinent Gondwana. Active migration of taxa in and out of the SO (depending on dispersal capabilities) caused a change in biodiversity composition of several invertebrate taxa over geological time scales including the period after the geomorphological isolation established. It is assumed that life on the seabed has not been completely erased at any time in the geologic past, although some taxa vanished while others thrived or radiated. Nowadays, natural and anthropogenically driven climate change processes shape the Southern Ocean marine fauna and we can only anticipate the threat associated with these changes because the processes driving speciation as well as biodiversity changes are not fully understood yet.

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25.1 Introduction

Antarctica is a continent of extremes and often provides particular conditions in terms of climatically induced ecological and physiological stress for biota (Peck et al. 2006). Nevertheless, over millions of years, a partly unique fauna has evolved, along with the continent and its physical environment since the disintegration of the supercontinent Gondwana. Thus, life in the Southern Ocean (SO) is well adapted to adverse conditions, and thrives even under "extreme" environmental challenges.

In the past decades, our knowledge on evolutionary adaptation in the SO, the unique environment, the changing ecological conditions, and the current and future threats has increased significantly (e.g. Barnes and Conlan 2007; Clarke et al. 2007a, b, 2009). This might be a suitable point at which to summarise the development of the Antarctic benthos under natural climatic and other evolutionary relevant conditions, determine briefly its status quo within the recent climate change situation and provide an outlook for future scenarios.

25.2 Environmental Background

The SO is limited to the north by an oceanographic front, the "Antarctic Convergence" or "polar fronal zone", which separates close to the sea surface cold Antarctic water masses (<4°C) from significantly warmer waters to the north. To the south, the SO is limited by the Antarctic continent. The clockwise flowing Antarctic circumpolar current (ACC) is the largest current system on earth and combines the three large oceans: the Atlantic, Indian and Pacific. The southerly adjacent Antarctic coastal current is flowing westwards counter-clockwise. The large vertical hydrodynamic processes are shaped by the down-welling of cold and saline water, mainly in the Weddell Sea, which expands into the SO deep sea even into the northern hemisphere and by the upwelling of warmer northern waters from intermediate depths. The SO seafloor covers an area of 34.8 million km^2. The shelves around Antarctica are on average 450–500 m deep, but exceed 1,000 m in places. From the total SO area, 4.59 million km^2 corresponds to continental shelf (<1,000 m), 2.35 million km^2 to continental slope (1000–3000 m depth), and about 27.9 million km^2 to the deep sea (>3,000 m depth) (Clarke and Johnston 2003). Thus, most of the SO is deep sea (~80%). Also, the Antarctic shelf comprises 17% of the world's total shelf area.

In winter, 60% of this 35 million km^2 large SO is covered by sea-ice. After the thaw in spring about 4 million km^2 remain. Together with the low and stable temperatures, this extreme seasonality shapes an ecosystem that depends on a moderately average, but highly variable primary production in the ice and open water. Enormous amounts of krill depend on this food source and provide the prey for higher organisms such as fish, penguins, seals and whales. Areas with less krill, few copepod species and some salps are major components of the so-called high nutrient–low chlorophyll (HNLC) pelagic system, which is being obviously, but not exclusively, limited by nutrients. At the seafloor, the benthos is surprisingly rich regionally both in species and biomass. Diversity of microbial life in the sediments is almost unknown.

25.3 Evolution and Climate Change

The Mesozoic opening history of the SO between South America, Africa and Antarctica is still one of the largest gaps in knowledge on the tectonic evolution of this region. After the separation of Africa, the break-up between Australia and Antarctica started approximately 100 Ma ago. This process successively led to the beginning of a deep-water circulation between Australia and East Antarctica, which was not completely developed before Eocene or Oligocene (approx. 55–35 Ma). At this time, the complete development of the ACC was only interrupted by the land bridge between South America and the Antarctic Peninsula. This large water mass already induced the cooling and glaciations of East Antarctica, and initiated the isolation of the marine shelf fauna. The circumpolar current became effective at the Eocene-Oligocene boundary due to the opening of the Tasman gateway (45 Ma), later of the Drake Passage approximately about 32.5–34 Ma, and the development of the Scotia Arc (Barker and Thomas 2004). This caused a further cooling of the SO surface water following the development of an extensive deep-water circulation between South America and the Antarctic Peninsula $\geq$30 Ma ago (Thomson 2004). These dramatic Tertiary palaeoceanographic changes (compare Brown et al. 2006) successively resulted in the generation of the psychrosphere, the cold Antarctic Deep Water (ADW), which is linked to the polar surface water in polar areas. These key events of cooling and glaciations of the continent shaped the evolution of many Antarctic marine species. The ADW is especially important to benthic organisms. It is partly generated at the SO ice margins, being cold, highly saline, and it might enhance the organisms migration potential from the shelf to the deep sea (polar submergence) and vice versa (polar emergence). The deep-water generation depends on sea-ice production, which is influenced by heat exchange at the atmosphere–ocean interface. If the ADW production was depleted or interrupted at any time in the past during interglacial periods, the barrier to colonisation would have been removed, and benthic organisms from lowest latitudes could have spread into the Antarctic. Geomorphologic investigations have documented past ice scouring to depths of at least 1,000 m, partly as a result of grounded ice shelves. However, there is evidence that benthic invertebrates survived the ice ages in refugia on the Antarctic shelf (Thatje et al. 2005; Leese et al. 2008), on the continental slope ($>$1,000 m depth) or at northerly adjacent islands and continental shelves. Some authors advocate the existence of productive oases such as coastal polynyas for the survival of marine species during glacial maxima (e.g. Thatje et al. 2008).

The cooling of the SO occurred rapidly at geological timescales. However, taking into account the ocean life, the temperature decrease with time equalled a cooling rate of 0.003°C within 1,000 years (Clarke and Johnston 2001). Even though this temperature change was very unlikely to have a catastrophic impact on benthic communities, many species became extinct, especially during the Late Cretaceous, while some survivors experienced a dramatic radiation. For example, krill, notothenioid fish (e.g. Eastman 2005; Di Prisco 2003), peracarid crustaceans and pycnogonids radiated in the SO, while decapod crustaceans, cirripeds or other teleostei are rare (Clarke and Johnston 2003). Benthic SO shallow-shelf faunas are archaic in structure and function, and modern predators, including skeleton-crushing (durophagous) bony fish, sharks as well as brachyuran crabs, are rare or absent (Aronson et al. 2007). Large invertebrates and epifaunal suspension feeders dominate many soft-sediment communities. The decreasing temperatures were probably responsible for the exclusion of the durophagous predators, and ultimately led to the endemic SO fauna with its unique food-web structure (Aronson et al. 2007). Sessile suspension-feeders are known to thrive, e.g. on the eastern Weddell Sea shelf, probably due to the coarse-grained and poorly sorted, glacial-marine sediments resulting from increased Antarctic ice extension with annual or cyclic retreats (e.g. Brandt et al. 2007a).

The Tertiary extinction of the decapod Reptantia is explained by physiological constraints related to haemolymph magnesium regulation capacities in the cold (Fredrich et al. 2001). The extinction of the Reptantia and most Teleostei, possibly related to climate change effects on these organisms such as reaching their oxygen and thermal tolerance limits (Pörtner and Knust 2007). This caused the emergence of new adaptive zones for other organisms. These events may have opened opportunities for spectacular adaptive radiations, for instance brood pouch bearing Peracarida (Crustacea, Malacostraca), whose brooding biology is discussed as a pre-adaptation to the SO climatic and biological changes (e.g. Pearse et al. 2009). Physiological and biochemical adaptations such as the development of antifreeze glycoproteins, the lack of hemoglobin as well as red blood cells, and free ecological niches supported the radiation of the notothenioid fishes. Also, it has been argued that Peracarida possess a variety of protective adaptations, which help reducing predation and enable these taxa to coexist with fish (Brandt 1999, 2000).

Latitudinal range shifts caused by plate tectonics, palaeoceanography and palaeoclimate changes (greenhouse to icehouse) impacted the SO marine fauna and flora and might have served as “taxonomic or climate diversity pumps” (Valentine 1973; Clarke and Crame 1997). These range shifts were accompanied by down- and upslope migrations of some eurybathic animals (Brey et al. 1996), and spatial isolation of true shallow water populations. Due to the ADW production, the Weddell and Ross Seas may be considered as important sources for taxa presently living in the Atlantic or Pacific deep oceans. This is because the isothermal water masses surrounding the Antarctic continent provide an obvious conduit for the migration of shallow-water species into more northern deep-sea basins. Investigations on the sea urchin *Sterechinus neumayeri* early larval stages pressure tolerance have demonstrated that these stages might be able to persist at depths deeper than 2,000 m (Tyler et al. 2000), and support the importance of the ADW even for the shallowest fauna.

Evolutionary radiation in isolation over long periods of time has led to levels of species endemism (60–90%) on the shelf, as reported for sponges, bryozoans (Barnes and Griffiths 2008), polychaetes, pycnogonids, ascidians, anemones (Rodriguez et al. 2007) and bivalves (Philobryidae; Linse et al. 2007). The isopod family Serolidae is likely to have originated some time between 90 and 55 my ago (Brandt 1991). Estimations for radiations in some taxa (Held 2000; Raupach et al. 2004) may coincide with geological processes. The inferred age of the last common ancestor of the iphimediid amphipod species is 34.4 million years, roughly coinciding with the formation of continent-wide ice sheets on Antarctica (Lörz and Held 2004). There is molecular evidence that some previously believed circum-antarctically distributed species are in fact cryptic species presently undergoing speciation processes. Examples within the isopod crustaceans are *Ceratoserolis trilobitoides* and the largest Antarctic isopod, *Glyptonotus antarcticus* (Held 2003). Recent investigations of deep-sea octopuses have shown that the SO acts as a centre of origin for these organisms (Strugnell et al. 2008), and the thermohaline express-way was used for the colonisation of the SO deep sea.

25.4 Modern Antarctic Benthic Biodiversity: Composition and Driving Forces

Benthic life of the SO and its biodiversity has already been the subject of many publications in an early exploratory phase of Antarctic research, and in the course of modern programmes such as European Polarstern Study (EPOS), Ecology of the Antarctic Sea Ice Zone (EASIZ) and Antarctic benthic deep-sea biodiversity: colonisation history and recent community patterns (ANDEEP), Census of Antarctic Marine Life (CAML), Evolution and Biodiversity in the Antarctic (EBA) and Latitudinal Gradient Project (LGP) (e.g. Dayton 1990; Hempel 1993; Arntz et al. 1997; Brandt 1999; Arntz and Clarke 2002; De Broyer et al. 2003; Clarke and Johnston 2003; Eastman et al. 2004; Balks et al. 2006; Clarke et al. 2006; Brandt et al. 2007a, b, c; Gutt et al. 2010).

25.4.1 The Shelf Environment

The Antarctic shelf inhabiting benthos has been geographically isolated for the last 30–35 Mio years, since deep-water basins opened between Antarctica and other fragments of Gondwana, the latest being Australia and South America (Lawver and Gahagan 1998; Thomson 2004). However, satellite images show gyres along the Polar Front which provide the potential for organisms to invade into and emigrate from the SO. Nevertheless, a biogeographic isolation of most, but not all, Antarctic shelf species is maintained by the sharp decline in sea surface temperature (SST)

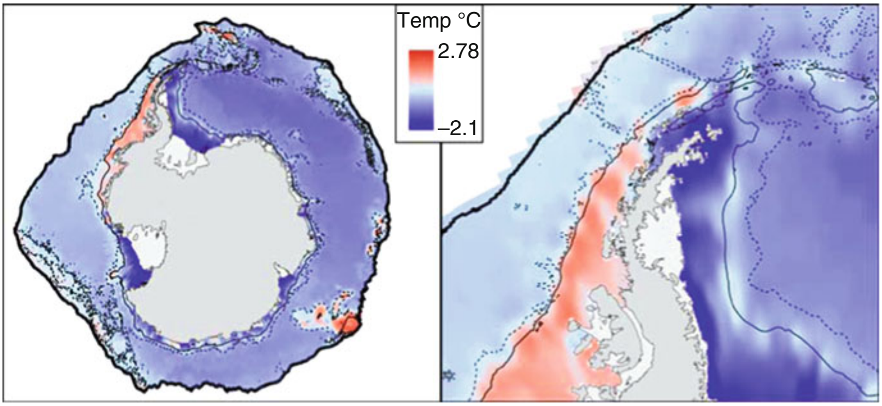

Fig. 25.1 Antarctic temperature. Spatial distribution of bottom (seabed) potential temperatures around Antarctica. (*left*) Circumpolar distribution of seabed temperature, emphasising the coldest temperatures on shelves closest to the ice shelves, and warmest temperatures of abyssal water in an eastward (*clockwise*) direction. (*right*) Detail of the Antarctic Peninsula, emphasising areas where shelves are warmed by the CDW from the ACC. Note the marked contrast between the Bransfield Strait and the outer shelf at the northern end of the Antarctic Peninsula. The 1,000 and 3,000 m isobaths are shown, and data extend to the mean position of the Antarctic Polar Front (from Clarke et al. 2009)

from between +8 and +10°C, e.g. around South America to less than 4°C off-shore and between −1.8 and +2.0 around the Antarctic continent. But, some species occur at South Georgia and the Antarctic Peninsula area, implying that these species must be able to tolerate widest temperature ranges (Fig. 25.1; Barnes and Peck 2008, Fig. 4a). Within Antarctic waters, both circumpolar current systems provide the potential for a fast dispersal of specimens and efficient gene flow. The East Antarctic shelf is exposed to the open ocean and only inner-shelf depressions and glacier tongues can act as barriers for species dispersal. Benthic habitats of the Western Antarctic Peninsula (WAP) are highly fragmented and have a complex current system; its seasonal sea-ice period covers a broad range from more than 9 months to only a few weeks. Here also warm intermediate deep water reaches the shelf more regularly compared with East Antarctic areas (Clarke et al. 2009).

One-third of the Antarctic shelf is overlain by floating ice shelves, consequently 46% of the coast line is formed by an ice front and a further 40% are covered by ice sheets (Gutt 2001; Clarke and Johnston 2003). The shallows below 25 m are shaped by the icebergs (Fig. 25.2), which destroy most of the epifauna each winter. Below this zone, diversity follows the intermediate disturbance hypothesis (IDH; Huston 1994) showing an increasing diversity with decreasing disturbance by ice scouring. At intermediate shelf depths between 50 and 250 m, the composition of assemblages hypothetically varies at almost all spatial scales as well as within higher taxa, and between larger systematic or functional groups (Gutt 2001). Various reasons for this patchiness are found in different regions, e.g. disturbance regimes can vary between environments. Moreover, food supply is an important

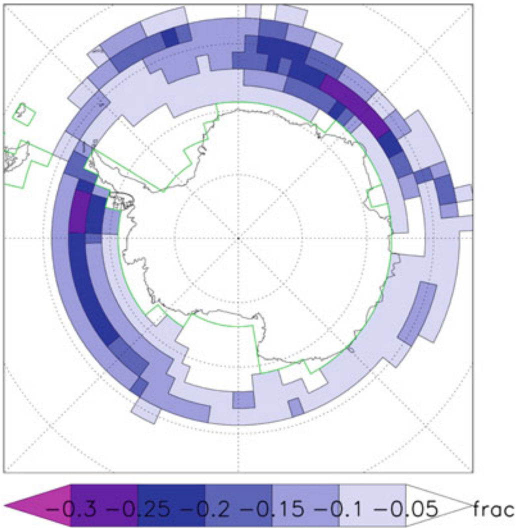

Fig. 25.2 Sea-ice prediction. Twenty First Century sea ice concentration change for the September–November period, showing the difference between the 2080–2099 mean and 2004–2023 mean. Changes are shown in terms of the surface fraction covered by sea-ice, rather than sea-ice percentage. Results and graph by T. Bracegridle, BAS, see also Turner et al. 2009

structuring factor in addition to substrates such as hard bottom (epifauna) or fine sediments (infauna). Although the sea-ice cover might not directly affect the deepest shelf benthos, it may have a strong impact on the sedimentation, including food, to the sea-floor. Similarly, the sediment or bathymetry may be a good indicator for the composition of benthic assemblages, although adult specimens of sponges, echinoderms and gorgonarians have surprisingly broad requirements in sediment characteristics. Filter feeders seem to benefit from food supply by high near-bottom current velocity, which also causes larger grain sizes in the sediment and expose hard substrata, whilst deposit feeders seem to prefer a less dynamic environment, where usually soft sediment habitats are found. While directly acting variables might be difficult to measure, indirectly acting parameters are well known and provide useful variables for bioregionalisation approaches (Beaman and Harris 2005; Grant et al. 2006; Koubbi et al. 2011). Gutt (2007) proposed a general classification for the Antarctic macrobenthos, in which the diversity of the filter feeder assemblage is relatively high not only because of the many sessile species, but also because these structure a three-dimensional micro-habitat for an associated fauna comprising amphipods and isopods, pycnogonids, holothurians, crinoids, gastropods, bivalves and nudibranchs, and also sessile encrusting species such as bryozoans and compound ascidians. The other main assemblage is dominated by the infauna, e.g. polychaetes or mobile deposit feeders such as holothurians or ophiuroids. Some isopods (Serolidae) or shrimps (*Notocrangon antarcticus*) are better adapted to this rather two dimensional habitat than their close relatives from the suspension feeder community such as Antarcturidae (Isopoda) and *Chorismus antarcticus* (Decapoda), respectively. In both assemblages, there are representatives that are relatively uncoupled from the unpredictable physical and biological processes in the upper water column (Gutt 2006; Mincks et al. 2005). This refers mainly to the melting of the sea-ice and the short period of primary production. Uncoupled meaning that, similar to deep-sea species, they can either respond in terms of feeding and reproduction to food supply events, or they can starve. Alternatively, species can benefit from energy stored in the sediment as a kind of “food-bank”, or have a flexible food preference allowing a feeding period that is much longer than the primary production phase (Barnes and Clarke 1995).

Applying the IDH to depths between 100 and 300 m, a maximum of diversity should be expected at an intermediate intensity of iceberg scouring. Results from surveys and modelling approaches have shown, however, that the undisturbed location is richest in diversity (Gutt and Piepenburg 2003). The reason might be that within the range of iceberg keels, an undisturbed equilibrium is rarely found due to the high intensity of disturbance. Only a few places exist where competitive displacement obviously leads to a reduced diversity in such final stage of benthic succession. Additionally, in undisturbed environments, many sessile species provide microhabitats for epizoans, which might compensate for the loss of outcompeted sessile species, and hide an existing effect of the IDH. In contrast to the local-scale disturbance, iceberg scouring causes an increase in biodiversity at the regional level due to the co-occurrence of different stages of recolonisation.

Assemblages shaped by trophic interactions are rare, maintaining a sensitive equilibrium between predators and prey, but they are well described for the McMurdo Sound by Dayton et al. (1974). Geomorphologically, the shelf edge is deep and varies between 500 and 800 m, however, the macrobenthos decreases in biomass and abundance at about 300 m depth with a few exceptions (e.g. corals; CCAMLR 2008).

25.4.2 The Deep-Sea Environment

The SO deep sea is characterised by a unique and highly diverse fauna of benthic invertebrates and exhibits some unique environmental characteristics, including a deep continental shelf, which can reach 1,000 m depth at places, and a weakly stratified water column. The SO is the source for much of the deep water in the world’s ocean. Due to these characteristics, the SO deep-sea faunas are related both to adjacent shelf communities and to those in other deep oceans. However, compared with SO shallow-water benthic communities, little is known about life in the vast deep-sea area of the SO. Today, it is still virtually impossible to obtain animals alive and undamaged from these depths. Therefore, we know almost nothing about the physiology, autecology or life histories of the SO deep-sea biota. True deep-sea benthic fauna occurs at depths between 1,500 and 2,500 m depending on the taxon. A deep-sea affinity of the Antarctic shelf has been described (e.g. Bullivant 1967; Dayton et al. 1974; Lipps and Hickman 1982; Brandt 1991; Brandt et al. 2007b). This can be explained by deep-sea species performing a polar emergence, or shelf species displaying submergence, and the eurybathy of the slope and deep-sea inhabitants (Brey et al. 1996). However, it must be stated that the shelf benthos and that of the adjacent slope and deep-sea differ from each other in most diversity parameters.

The geographic focus of the recent ANDEEP (ANtarctic benthic DEEP-sea biodiversity: colonisation history and recent community patterns) project were the Scotia and Weddell Seas (Brandt et al. 2004). This region is characterised by a complex tectonic history, being sited close to the Bouvet Mantel Plume where the break-up of the Gondwana supercontinent began around 180 Ma ago, (Storey 1995). Thus, the Weddell Sea developed at the focus of radial seaways, spreading out to become the Indian and South Atlantic oceans. The Weddell Sea seafloor dates back to the Middle Jurassic, whereas the Scotia Sea formed much later, during the last ~40 Ma (Thomson 2004), a potential reason (age) for the relatively high level of species richness in the Weddell Sea (Brandt et al. 2007a, b, c). The ANDEEP expeditions have sampled across a broad range of taxonomic groups, representing meio- to megafaunal size fractions, and documented substantial levels of novel biodiversity. For example, the Foraminifera were represented by 158 live species, the nematodes belonged to typical cosmopolitan deep-sea genera, but more than half of the 57 species recognised in selected genera were new to science, and more than 100 ostracod species were distinguished, >70% of them new (Brandt et al. 2007b). Macrofaunal isopods were highly diverse with 674 species identified, compared with 371 species reported from the entire Antarctic continental shelf (Brandt et al. 2007a, b, c). More than 200 polychaete species were recognised, 81 of them previously unknown (Schüller and Ebbe 2007). Our samples yielded 160 species of shelled gastropods and bivalves compared with 279 species known from the shelf (<1,000 m) (Brandt et al. 2007b). Seventy-six species of megafaunal sponges were recognised, 17 of them were new to science and 37 new for the SO (Brandt et al. 2007b; Janussen and Tendal 2007). However, in future, we need to test whether the high biodiversity can be explained by the age of the Weddell Sea or the fact that this is a major source for the world’s deep-water production.

The application of molecular biological techniques showed that some of the traditionally regarded circumantarctically distributed species are in reality composed of several cryptic species, e.g. Isopoda, Serolidae (Held 2003) or *Lissarca notocardensis* (Linse et al. 2007). The existence of such “species flocks” in the deep-sea biota may be a more general feature than is currently assumed (e.g., Raupach et al. 2007), implying that the high species richness documented might even increase in future.

The ANDEEP expeditions have also revealed some unique features and strong contrasts between deep SO faunas and those from other oceans. In particular, isopods are distinctive with many species currently unknown outside the SO (~90%). Among the vagile family Munnopsidae comprising 50% of all isopods sampled during ANDEEP at 40 stations as well as in other important SO taxa (e.g. Desmosomatidae, Haploniscidae and Ischnomesidae), >95% of the ANDEEP species are undescribed. While we know that some species complexes have radiated in the deep SO (e.g. the Haploniscidae; Brökeland and Raupach 2008), it is unclear whether they have evolved here and subsequently spread into other ocean basins. The few SO deep-sea isopod species that have been described show closest biogeographical links to Atlantic faunas. Many ANDEEP ostracod species are presently unknown outside the SO, e.g. the ostracod family Macrocyprididae was common in the ANDEEP material, but usually rare in deep-sea samples from other oceans. The majority (~75%) of mollusc species were also unknown outside the SO and wide-ranging Atlantic deep-sea species, such as the gastropod *Benthonella tenella,* were not collected. Polychaete families (Spionidae, Paraonidae and Cirratulidae), which are common and species-rich at temperate latitudes, were rare meaning represented by few species in the SO deep sea. Many SO nematode species are new and apparently confined to particular parts of the Weddell Sea, although some have wider distributions. These biogeographic patterns may be linked to reproductive strategies. The isopods, ostracods and nematodes have poor dispersal capabilities and hence reduced gene flow, making restricted species distributions and highest degrees of endemism explainable (Brandt et al. 2007b).

25.5 Ecosystem Services of Antarctic Biodiversity

The Antarctic benthos (Figs. 25.3 and 25.4) must be seen as an integrative part of the world's marine biodiversity especially in the light of its regional and global threats. Antarctic pycnogonids and also to a lesser extent polychaetes contribute above average to the world's species richness relative to the size of large habitats Clarke and Johnston 2003). These taxa contradict the hypothesis of latitudinal gradients in species richness. Such a gradient seem to be less obvious in the southern hemisphere and vary considerably between different systematic groups. For the deep sea, there is additional evidence within several taxa such as isopod crustaceans, gastropods or sponges that species richness is not depressed in the SO abyssal compared with the northerly adjacent deep-sea basins (e.g. Brandt et al. 2007b).

Even if the psychrosphere of the SO shrinks as predicted in the coming decades, Steig et al. (2009) documented that West Antarctic warming exceeds 0.1°C per decade over the past 50 years. Coastal waters at all depths might provide a refuge for cold-adapted species since the huge continental ice cap will block a significant warming in coastal waters. However, we have no idea how a decrease of the Antarctic ice sheet (Fig. 25.2) might affect deep-water production and will ultimately begin to influence the SO deep-sea temperature and food availability. The highly endemic fauna, which has adapted to the climate changes associated with the disintegration of the Gondwana continents over millions of years, is reason enough to protect this unique and pristine environment and its inhabitants. Moreover, the SO deep-water production nourishes the world oceans and functions as a promoter for our present-day (contemporary) ocean currents.

New results on global CO_2 budgets and large-scale oceanographic circulation patterns provide important hints that the Antarctic benthos, together with other components of a global marine ecosystem, might play an important role in this context. Carbon is not subtracted from the global budget when biologically

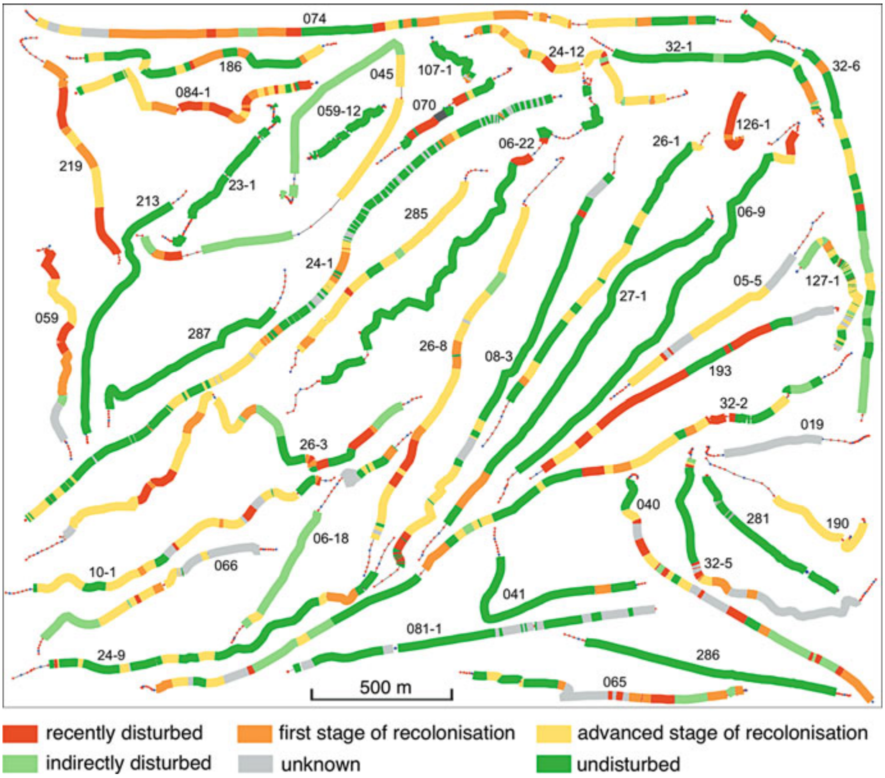

Fig. 25.3 Schematic illustration of different stages of iceberg scours on the seafloor of the Weddell Sea. Videotransects from the Eastern Weddell Sea at water depths between 150 and 450. The colour coded classification according to Gutt and Starmans (2001) illustrates the fragmentation of the benthic habitat when exposed to iceberg scouring. Results of statistical analyses based on representative scenarios show that such heterogeneity (beta-diversity) can cause increased regional (gamma) diversity (Gutt and Piepenburg 2003). For supplementary data see doi: 10.1594/PANGAEA.755488, doi: 10.1594/PANGAEA.755491 and dio: 10.1594/PANGAEA.755490

incorporated in benthic organisms. Upwelling processes can bring CO_2 resulting from benthic respiration back to the sea surface. Thus, benthic processes determine whether and how the organic matter that sank to the seafloor will be fixed for millions of years in biogenic sediments or be recycled. Such processes depend on the composition of species, which can be dominated by highly dynamic populations of, for example, ascidians and some sponges (genera *Homaxinella* and *Mycale*) or by organisms with extremely low metabolic rates, such as adult hexactinellid sponges (Gutt et al. 2010, 2011). Representatives of both demo- and glass sponges fix high amounts of silicate-derived opal in their skeleton, and eventually in so-called sponge-spicule mats after their death. Consequently, a specific part of the Antarctic benthos, together with the plankton, influences the silicate-cycle,

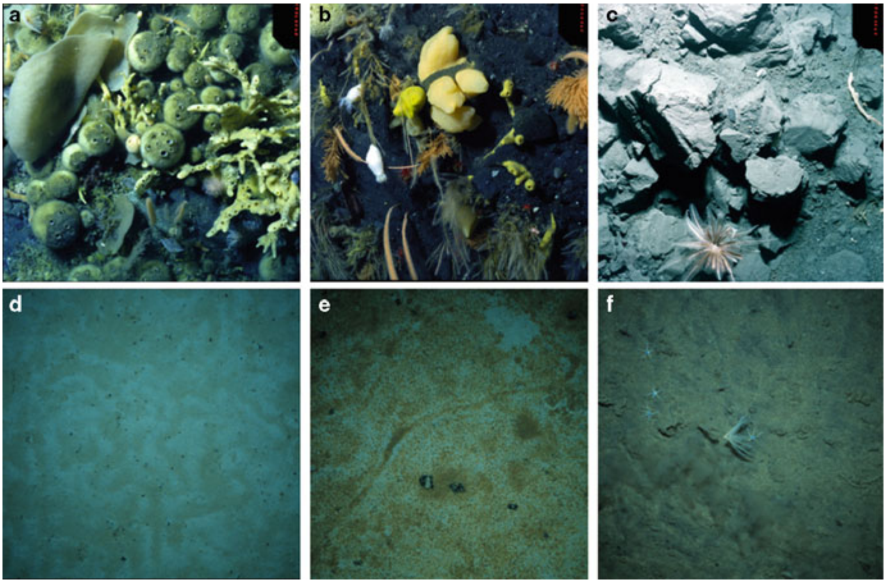

Fig. 25.4 Photographs from the Southern Ocean seafloor. *Upper row* (**a**–**c**) examples for the Antarctic shelf, *lower row* (**d**–**f**) examples for the Southern Ocean deep sea. For (**a**–**c**): photograph: J. Gutt, © AWI/Marum, University of Bremen; for (**d**–**f**): photograph: R. Diaz, © VIMS, Virginia, USA. (**a**) Extremely dense concentration of demosponges (with several ocula) and hexactinellid sponges (*vase-shaped*), bryozoans, and compound ascidians provide the microhabitat for a shoal of *Trematomus* fishes. Water depth 160 m. (**b**) Sea-bed at 80-m water depth, recently disturbed by a grounding iceberg. Only two pycnogonids invaded so far due to their mobile life mode. (**c**) Sea-bed at 80-m water depth, recently disturbed by a grounding iceberg. Only a crinoid so far invaded due to its mobile life mode. (**d**) Sea-bed in 3,535 m depth in the western Weddell Sea showing very fine sediment with organic matter which has been partly consumed by animals. (**e**) Sea-bed in 2,773 m depth in the western Weddell Sea fluff (organic matter). (**f**) Sea-bed in 6,348 m depth in the South Sandwich Trench showing a stalked crinoid (*Bathycrinus*) as well as ophiuroids

driven by the growth of diatoms and some sponges, which also determines significantly the capacity of the SO as a biological CO_2 sink.

25.6 Ecological Response of Benthic Biodiversity to Recent Climate Change and Other Threats

The West Antarctic Peninsula (WAP) is experiencing one of the fastest rates of regional climate change on Earth, resulting in the collapse of ice shelves, the retreat of glaciers and the exposure of new terrestrial habitat (Clarke et al. 2007a, b). The atmospheric warming at WAP is four times above the global average, as a result of increasing westerly winds due to unknown, most likely non-anthropogenic reasons.

Present temperatures on the continental shelf can range between freezing point at −1.8°C or slightly below, e.g. in the Weddell and Ross Seas, and +2.0°C in West Antarctic waters (it can be higher locally, see Barnes and Peck 2008). During an early Holocene climate optimum and in a period previous to that, interglacial atmospheric temperatures were occasionally above present values (for background information see Turner et al. 2009). As a consequence, sea-ice extended less to the north compared with the recent average winter maximum. Sea-surface temperature (SST) was slightly warmer than today (Crosta et al. 2004), but did not considerably exceed the range of the 1.3°C warming, which has been observed West of the Antarctic Peninsula since 1955 (Meredith and King 2005). Natural climate events in the Holocene with a high potential to impact the ecosystem must have caused the multiple collapses and advances of ice shelves West and East of the Antarctic Peninsula such as the Larsen A ice shelf (Domack et al. 2005). Also a complete disintegration of the West Antarctic Ice Sheet in the past interglacial has been suggested (Mercer 1968). Deeper water masses are generally characterised by their high stability of temperature. However, significant changes in the species composition between glacials and interglacials are found, and attributed to the changes in the thermohaline circulation, temperature, food and pelago-benthic coupling (Cronin and Raymo 1997).

As a result of the above described long-term evolutionary processes, most benthic species found today in the SO are physiologically adapted to the conditions of glacials as well as interglacials, and also to a relatively fast switch between both, as they experienced such cycles nine times in the past Mio years. Animal temperature limits and its ecological relevance, depending on the size and activity of the organisms and rates of change, has just been reviewed by Peck et al. (2009). Since many of the endemic and non-endemic species are regionally successful, most of them cannot be assumed to live at the limit of their ecological or physiological tolerance. Exceptions might be decapod crustaceans due to a specific manganese metabolism (Fredrich et al. 2001).

In contrast to the shelf fauna, a possible limitation of the SO deep-sea fauna by environmental conditions is difficult to assess. The high number of SO endemic deep-sea species (Brandt et al. 2007a, b) indicates that these are unlikely occasional guests which have their main distribution areas and reproduction centres further north or at continental slopes according to the “source-sink-hypothesis” by Rex et al. (2005). Smith et al. (2008) have reviewed abyssal food limitation, ecosystem structure and climate change, and emphasise the importance of monitoring and modelling efforts. Estimations of regional endemism can serve as a basis for the evaluation of the likelihood of species extinctions from regional changes in abyssal food availability; the latter engendered by climate change and coupled with SO deep-water production. A problem with the impact assessment on deep-sea communities is that we do not know the drivers of biodiversity there, and how these influence deep-sea assemblages.

A similar situation and an unusually high number of deep-sea species are found under ice shelves in shallow waters, either investigated through drill-holes or after their climate-induced disintegration (Lipps et al. 1979; Post et al. 2007; Gutt et al. 2011).

The recent mainly anthropogenically driven global atmospheric warming is superimposed in the Antarctic and partly blocked by other effects (for a comprehensive compilation of detailed results see Turner et al. 2009, for review see Convey et al. 2009). The East Antarctic has shown slightly decreasing or stable temperatures in the past decades leading to an increasing sea-ice cover most likely consequent from the ozone hole. Recruitment patterns of organisms in Antarctic Peninsula shelf sediments are decoupled from seasonal phytodetritus pulses (Mincks and Smith 2007). Year-round recruitment is consistent with the presence of a persistent "food bank" in WAP shelf sediments, allowing recruitment to be largely decoupled from seasonal bloom dynamics. Deep water masses show temperature changes within a range of only a few 0.01°C in the past decades (Fahrbach et al. 2004; Johnson et al. 2007), which must be considered to represent, thus far, very stable conditions in a biological context. The recent collapses of ice shelves are affected west of the Antarctic Peninsula by the upwelling of warm water and east of the Peninsula by an atmospheric warming (Turner et al. 2009). A significant acidification of the SO following as a result of increasing atmospheric CO_2 has not been measured yet. However, simulations show that the pressure-dependent natural saturation horizon (Carbonate Compensation Depth, CCD) has moved closer to the sea-surface (Orr et al. 2005), and many species are unable to build up calcium carbonate skeletons below the CCD.

Until now the most obvious response of the SO ecosystem to climate change has been observed for those components that are closely linked to the sea-ice and its dynamics: the growth of algae, the recruitment of krill and the population dynamics of penguins. For zooplankton groups other than krill, a change from larger to smaller species was observed around 2,000 m in East Antarctic waters, but this cannot be reliably correlated to a warming or a significant change in ice dynamics (Gutt et al. 2010). Evidence for a response of the SO benthic system to the recent climate change is rare. The most significant climate-induced change in environmental conditions for bottom inhabiting animals is that of collapsing ice shelves. A first ecological survey carried out 5 years after such an event in Larsen B and 12 years after that at Larsen A east of the Antarctic Peninsula revealed hints that pioneer species such as ascidians grew to an adult size after the collapse and occurred in high density, whilst a possible temporary aggregation of the deep-sea holothurian *Elpidia glacialis* can be explained by the increased food availability and successful reproduction. An extreme proportion of small hexactinellid sponges indicate that the formerly oligotrophic system is permanently changing to a normal situation, which perhaps in a later stage will be dominated by such sessile suspension feeders (Gutt et al. 2011). In some cases, it is generally difficult to explain shelf communities by recent environmental conditions as it is nearly impossible to observe such long-term colonisation processes. If populations of deposit feeders such as *E. glacialis* persist, sessile assemblages might permanently have difficulties in establishing themselves, a phenomenon called trophic ammensalism. In other pristine areas with successful recruitment and growth especially of young sponges, such a "spiny" environment will keep fragile deposit feeders away for long periods. There is no doubt that retreating glaciers releasing terrigenous sediments and an increased fresh water runoff into coastal waters have already had an effect on benthic biota on a local scale. However, Philip and Abele (pers. comm.) found that the clam *Laternula elleptica* has been mostly unaffected.

Extensive monitoring programmes are missing for the measurements of changes in benthic populations or communities. Even the occurrence of stone crabs West of the Peninsula only provides the basis for speculations on the actual climate-induced invasion of Sub-Antarctic and South American species (Aronson et al. 2007).

In contrast to biological long-term and large-scale processes, our knowledge of past and future development of the physical environmental is fairly good. Also, to predict biological changes, we must increase our efforts in field surveys, experiments and learn more about the tolerance of true ecological key species as representative of the majority of benthic species. Besides, we have to learn more about the food-web composition, especially in the SO deep sea. Thus far, we can only rely on a few valuable physiological and behavioural studies or deduce the overall tolerance of the system based on natural variability to which species are naturally exposed. On this basis, we would like to speculate here about the future of the Antarctic benthos.

Changes in both sea ice cover and iceberg production around parts of west Antarctica are likely to have a strong influence on biodiversity. Increasing scouring by icebergs on the shelf (an example of different stages of ice scours is documented in Fig. 25.5) is likely to increase regional biodiversity in areas that are not already exposed to intensive disturbance (Johst et al. 2006). In contrast, scouring could drastically reduce local and regional biodiversity in the shallows (top 50 m). Later, when icesheets retreat past grounding lines, disturbance may reduce around the WAP because of decreased calving to sea and thus icebergs. This might decrease regional, but not local diversity and only a very few species (such as some pioneers), which depend on the ice scours, will become endangered. However, if competition is as hierarchical as other biologists suggest a few strong competitors may monopolise virtually all space in the shallows.

If ice shelves continue to disintegrate, further under-ice shelf habitats will be lost in terms of their unique environmental conditions, species composition and ecosystem functioning. This includes organisms so far identified as representatives of true deep-sea species. Species occurring endemically at specific ice-shelf sites will definitely vanish. However, it must be stated that at present no simulation of the physical environment predicts the complete collapse of the large ice shelves, so this Antarctic-specific habitat will not generally be lost.

If temperature continues to increase, benthic shelf species have – as in the past – the potential to retreat to or survive at greatest depths and in more southern areas where warming can be excluded or is less pronounced, in other words range shifts have to be expected (Barnes et al. 2009). Alien species are prevented from invading Antarctic shallow waters as long as the steep gradient in SST between warmest water masses north and coldest masses south of the Polar Front persists (Clarke et al. 2005). The predicted 1°C increase until 2100 (Fig. 25.2, Bracegirdle et al. 2008) will remain below a threshold that makes the temperature-barrier generally more permeable. This, however, does not necessarily mean that single species

Fig. 25.5 Antarctic free-living isopods and amphipods represent evolutionary radiation and adaptation to various discrete ecological niches. Isopods: *upper row* (© T. Riehl, Zoologisches Museum and M. Rauschert, AWI), from *left* to *right*: *Cuspidoserolis meridionalis* (6 cm), *Sursumura angulata* (2.2 cm, *upper*), *Paranthura antarctica* (3.5 cm, *lower*), *Eurycope* sp. (approximately 0.7 cm). Amphipods (© M. Rauschert, AWI): *central row*: *Eusirus perdentatus* (5 cm), *Melphidippa antarctica* (2 cm), *Eurythenes gryllus* (approximately 10 cm), *bottom*: *Paraceradocus gibber* (8.5 cm), *Epimeria robusta* (3 cm), *E. rubrieques* (4 cm)

might progressively invade, or species will enlarge their zoogeographic distribution within the Southern Ocean, colonise larger areas and replace the original fauna locally.

A change in primary production providing food directly or indirectly for the benthos can be expected as a consequence of a reduced sea-ice extent and a warming of the SST acting most efficiently at lower latitudes between 55 and 60°S (Arrigo and Thomas 2004; Sarmiento et al. 2004; Turner et al. 2009). If the deep-sea fauna is food limited not only in its abundance/biomass but also in its diversity, a possible consequence would be an increase in these both variables (Smith et al. 2008). If the condition of a temperate system during a glacial period could act as a case study for the future of the Antarctic, it can be expected that the retreat of the sea-ice in a period of warming and, consequently, a shift in the pelagic community would be mirrored on the sea floor, e.g., in the ostracod and diatom composition (Cronin and Raymo 1997).

In the worst case scenario of a complete lack of sea ice, an increase in primary production of 25% would probably affect the shelf benthos more negatively than a decrease. Before this scenario becomes reality, intermediate stages of changes in the trophic conditions are possible for which the complex response west of the Antarctic Peninsula can be an example (Montes-Hugo et al. 2009). On the shelf, such a possible regional decrease of food might not become a big problem for most species. Probably, most benthic species also survived on the shelf at a 90% reduced food supply during LGM (Bonn et al. 1998) and, consequently, have a high potential to endure these periods. Because krill faecal pellets are heavy and sink rapidly to the sea floor, a continued decrease of krill (Atkinson et al. 2008) could on the one hand reduce the food supply to the seabed. In that case, the pelagic system could shift from a so-called export-system to a recycling system (Peinert et al. 1989) with a shift to a more oligotrophic situation for the benthos, even in the deep sea. However, if phytoplankton growth increases rather than decreases and is not grazed by krill, huge amounts of phytodetritus not consumed or recycled in the upper water column would slowly reach the sea floor. It is difficult to predict the benthic response in a non-trophically limited shallow or deep system, but it seems most likely that only a limited number of species would benefit, and consequently the diversity would change or even decrease. It also seems to be more likely that deposit feeders rather than filter feeders would benefit from such a situation, since the latter are supposed to be sensitive to an unusual surplus of food by clocking their feeding apparatus. Consequently, if the filter feeders suffer, negative cascading effects are also expected for the rich-associated fauna. The same scenario can also be applied to the deep benthos, but with the possible difference that firstly the deep environment will change from a trophically limited system to a saturated one before diversity decreases, and the system shifts from that dominated by specialists to opportunists.

Acidification might become one of the largest problems for the SO ecosystem, in the pelagic and benthic realm. As a consequence for the increasing atmospheric CO_2, most of the SO is expected to become undersaturated until 2100 in both calcium carbonates, aragonite and calcite, the first being the major component of molluscs and corals skeletons, and the latter that of coccolithophorids (Orr et al. 2005). On a vertical axis, the threat comes from both sides: from the sea surface because it is directly exposed to increased CO_2 and from deepest water layers because saturation principally decreases with increasing pressure. Consequently, the deep sea is undersaturated as is most of the Antarctic shelf. The polar oceans are especially threatened because calcium carbonate saturation is positively correlated with temperature and the uptake of atmospheric CO_2 is above global average. Despite the lack of a general understanding of ecological consequences for benthic systems, it is generally known that the problems for organisms in building up their skeletons is species specific, some such as sea urchins suffer, but some even seem to benefit, e.g., tunicates (Dupont and Thorndyke 2009). It has to be considered that such animals are extremely rare in the deep sea and that many shelf-species, which regionally shape the entire benthos, e.g., echinoderms, hydrocorals and gorgonians belong to the potentially threatened calcifying organisms.

25.7 Future Demands on Southern Ocean Climate-Related Ecosystem and Biodiversity Research

The substantial efforts to increase our knowledge on climate change in the past decades showed that some important changes in physical parameters can be detected relatively easily, using remote sensing techniques with a high spatial and temporal resolution and a large spatial coverage. The response of ecosystems including their biodiversity and functioning, however, is still very poorly understood because of the immense complexity of biological systems (Clarke et al. 2007b), and maybe because of a certain delay between physical processes and the biological response. However, decision makers demand a good knowledge on biological changes and expect predictions. A strategic scenario for the Antarctic ecosystem would be concerted international monitoring of selected SO sites, e.g. West and East of the Antarctic Peninsula or SO deep sea. Single initiatives of this kind have already existed for a long time, which mainly focus on living resources, such as krill, fish and some mammals, and are coordinated by the Convention of the Conservation of Antarctic Living Resources (CCAMLR). At such sites not only faunistic surveys could be conducted, but also the complex drivers behind Antarctic benthic diversity could at least partly be deciphered in the light of changing environment. Results, however, being representative for largest parts of the entire SO cannot be obtained without large-scale surveys, and corresponding compilations of existing results in data bases. Despite internationally combined efforts during the successful International Polar Year 2006–2007 and the Census of Antarctic Marine Life (CAML), large areas of the SO, especially in the deep sea and also on the shelf under the ice-shelves and in the Amundsen/Bellingshausen Seas are almost unknown (Kaiser et al. 2009). In cases where field studies cannot be performed, predictive environment-diversity coupled simulation-models have to be developed. Such models demand a much better knowledge on the ecological and physiological tolerance as well as life history traits of true ecological key species. Diversity analyses would greatly benefit from fastest species identification by combined morphologic and genetic methods.

25.8 Conclusion

Yasuhara et al. (2009) document latitudinal gradient dynamics and tropical instability of deep-sea species diversity. They found that an unexpected instability and high amplitude fluctuations of species diversity in the tropical deep sea were correlated with orbital-scale oscillations in global climate. In their study area, species diversity was low during glacial maxima and increased or even high during interglacial periods. We have to assume an even highest impact in the SO deep-sea ecosystem, which will be strongly influenced by warming in terms of a reduction of the ice sheet and sea-ice generation, the strongly coupled deep-water production, and the benthic food supply. In the SO, deep sea regional abyssal warming and acidification may not be detected for some time due to the buffering effect by the huge volume of water (Kaiser and Barnes 2008). From recent investigations on the effect of climate change on the ecosystems however, we have to deduce that increased sea-surface temperature, increased thermal stratification and ocean acidification will reduce primary production, change the quality and quantity of organic carbon fluxes, and ultimately alter the structure and function of abyssal ecosystems (Smith et al. 2008). Even though there is no doubt that primary production and food availability will regulate and alter abyssal biodiversity, we do not know how a shift in structure and function of abyssal ecosystems will take place and the many unknown factors will prevent explicit predictions of the effects.

The SO marine fauna has adapted well to the changing climate over the last 30–35 million years, even though some faunal elements became extinct while others thrived, or even radiated on the Antarctic continental shelf as well as in the SO deep sea. Therefore, we have to conclude that climate change will not erase the SO marine fauna, neither on the shelf nor in the deep sea. However, due to recent physiological and ecological investigations, we have to expect biological changes, for example, a shift in species composition and the food-web structure. However, currently, it is impossible to estimate to which extent these alterations will happen. A prerequisite for environmental protection of any SO organism is the understanding of the regional biodiversity and processes generating and maintaining it.

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Part VI
Conclusions

Chapter 26
Biodiversity Hotspots: Concluding Remarks and Perspectives

Frank E. Zachos, Russell A. Mittermeier, and Jan C. Habel

The preceding 25 chapters addressed the topic of this book, biodiversity hotspots *sensu lato*, i. e. geographical areas with high levels of endemism or species richness, high numbers of threatened species and facing intense threats (Reid 1998), in various ways. As outlined in the Preface, we are aware that the issue, inevitably, has not been covered in its full breadth and depth. Nevertheless we hope that the present volume as a whole will be a valuable and fruitful contribution to the future research on biodiversity and its conservation. We are especially proud that it contains the original publication on the 35th biodiversity hotspot *sensu stricto*, the Forests of East Australia (Chapter 16, Williams et al. 2011).

The majority of chapters deal with terrestrial regions in the tropics, which is in line with Brooks et al. (2006) who found that it is particularly tropical (and Mediterranean-type, see Chapter 7, Hewitt 2011) environments that are emphasized as priorities for biodiversity conservation irrespective of the prioritization template applied. However, two main biases cast a shadow on our present evaluation of global biodiversity, its distribution, and conservation. All such studies hinge on some kind of diversity quantification (of which there are many, see Magurran 2004; Chapter 3, Davies and Cadotte 2011), and this quantification almost exclusively relies on diversity in plants and vertebrates. The second bias is the almost exclusive consideration of terrestrial environments, while more than 70% of the earth's surface is covered by water. In both cases, of

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course, researchers have to make a virtue out of necessity because they have to rely on available information which is heavily biased toward plants, vertebrates and the terrestrial realm. Here, there is an urgent need for more primary data on marine, fungal, invertebrate, and microbial diversity. Prioritization of areas based on arthropods (by far the most diverse invertebrate taxon) and that based on plants and vertebrates do not always match well, but results differ among studies (Brooks et al. 2006 and references therein; Chapter 11, Bálint et al. 2011), and further directly comparable studies are much needed. Compared to biodiversity research in terrestrial environments, the study of marine biodiversity is still in its infancy, but efforts are increasing, in particular with respect to one of the planet's megadiverse ecosystems: coral reefs (Roberts et al. 2002). Reaka and Lombardi (2011, Chapter 24) present a review on coral reef biodiversity, which is more threatened than rainforests, and Brandt and Gutt (2011, Chapter 25) address deep sea biodiversity, a topic that was only recently incorporated in the analysis of global biodiversity.

Therefore, while the above-mentioned biases are reflected by the content of this book, we are pleased to also have chapters covering areas that are less well-studied but that have great bearing on global biodiversity and its protection. This also holds from a taxonomic point of view. While 9 out of 11 taxon-specific chapters cover plants or vertebrates, we do have two chapters dealing with invertebrates, carabid beetles in the Palaearctic (Chapter 10, Schuldt and Assmann 2011) and aquatic insects in the Carpathians (Chapter 11, Bálint et al. 2011).

Even many classical, i.e., terrestrial plant and vertebrate hotspots are comparatively understudied. Maybe *the* primary example is insular Southeast Asia and Melanesia which have within its borders 4 of the 35 global biodiversity hotspots *sensu stricto* (Indo-Burma, Sundaland, the Philippines, and Wallacea; Chapter 1, see Mittermeier et al. 2011; Sodhi et al. 2004) and is *the* hotspot for marine diversity, particularly the famous Coral Triangle in Indonesia, Malaysia, the Philippines, Timor Leste, New Guinea, and the Solomon Islands (Chapter 24, Reaka and Lombardi 2011; Roberts et al. 2002). Southeast Asia is very rich in endemics, e.g., nearly 60% of all Indonesian vascular plants occur nowhere else (Sodhi et al. 2004), and sadly, the region also harbours the highest numbers of threatened vertebrates (both terrestrial and aquatic, Hoffmann et al. 2010). Two contributions of the present volume (chapters 19 and 20) cover Southeast Asian vertebrates: Pagès et al. (2011) present research on rodent diversity within and among species, and Koch (2011) summarizes our knowledge about the herpetofauna of Sulawesi, highlighting that even in comparatively well-studied groups like amphibians and reptiles, biodiversity has been significantly underestimated. The prospects of Southeast Asian biodiversity have been called "an impending disaster" by Sodhi et al. (2004). These authors conclude that Southeast Asia might lose 75% of its original forests by the year 2100 and up to 42% of its biodiversity. The main threat drivers include forest conversion (but see Edwards et al. 2011 for the value of even repeatedly logged forests in the region), wildlife trade, and bushmeat hunting.

It is becoming increasingly clear that the future of biodiversity conservation critically depends on the integration of local and regional socioeconomic and cultural aspects. This is because human populations in areas of high biodiversity are still growing (see Chapter 4, Williams 2011) and because in practice enforcement of conservation strategies hinges on the acceptance and ownership by local people. This is outlined for Madagascar by Fritz-Vietta et al. (2011, Chapter 12) and for Ecuador by Rieckmann et al. (2011, Chapter 22), and it certainly holds globally as well (Rands et al. 2010).

The target of the 1992 Convention on Biological Diversity (CBD) was to significantly reduce the rate of biodiversity loss by 2010. The CBD was subsequently incorporated into the Millennium Development Goals (MDG) of the United Nations. In 2010, a number of studies and reviews were published assessing the successes and failures of the CBD. Not surprisingly, the latter preponderate by far. Stokstad (2010) summarizes the results and concludes that with regard to habitat degradation, conservation status of species, conservation funding and invasive species management "some" progress has been made, while in particular with respect to (harmful and unsustainable) consumption of biological resources more or less nothing has been achieved. "Significant" progress has been made concerning the extent of protected areas: globally, 12.9% of all land is under some kind of protection, but this only holds for 0.5% of the oceans so far (Stokstad 2010). Often, however, the progress made cannot conceal that the efforts to date have clearly been insufficient. Hoffmann et al. (2010) show that about 20% of all vertebrate species are classified as threatened by the IUCN (for amphibians this value is even 41%) with on average more than 50 species of mammals, birds and amphibians moving one category closer to extinction annually. They also state very clearly that "for any single threat, regardless of the taxa involved, deteriorations outnumber improvements; conservation actions have not yet succeeded in offsetting any major driver of extinction risk" (p. 1508). Nevertheless, these authors also estimate that the rate of deterioration would have been one-fifth or more higher without conservation efforts, which stresses that future prospects are not necessarily bleak if further efforts are made. These efforts are urgently needed as future species extinction rates might exceed recent rates by 2 orders of magnitude or more (Pereira et al. 2010). Butchart et al.'s (2010) conclusion is in the same vein when the say that apart from coral reef condition (for which decline has been constant since the mid-1980s), no indicator of the state of biodiversity shows a significant reduction in decline and that there is "a growing mismatch between increasing pressures and slowing responses" (p. 1168).

At the latest Conference of the Parties of the CBD, held in Nagoya, Japan, in October 2010, even stronger targets were proposed and accepted as part of the Strategic Plan for the period 2011–2020. Of the 20 "Aichi Biodiversity Targets" (see Appendix), Targets 11 and 12 are particularly noteworthy. Target 11 increases the protected area target to 17% for the terrestrial realm, a 4% increase over where we are today, and the marine target to 10%, which represents an order-of-magnitude leap in coverage. If the 4% is strategically selected, it will cover the current gap in protected areas coverage in highest priority areas like the hotspots. This is very encouraging.

The bleak conclusion, in spite of some achievements, is that immense loss of biodiversity will continue unless very strong measures are put in place at a global level. What is more, much of this loss will be concentrated in the hotspots. Preventing this is not only a moral issue but also a very practical one as the economic value from biodiversity has recently been estimated to be 1–2 orders of magnitude higher than the costs of maintaining it (Rands et al. 2010 and references therein), with the recent TEEB report providing a particularly strong case (Sukhdev et al. 2010).

Appendix

List of the 20 biodiversity targets ("Aichi Biodiversity Targets") proposed for 2011–2020 at the CBD conference in Nagoya, Aichi, Japan, in October 2010. There are five Strategic Goals A–E with a number of specific targets assigned to each of these goals. Source: Convention on Biodiversity internet homepage, http://www.cbd.int/sp/targets.

Strategic Goal A

Address the Underlying Causes of Biodiversity Loss by Mainstreaming Biodiversity Across Government and Society

Target 1. By 2020, at the latest, people are aware of the values of biodiversity and the steps they can take to conserve and use it sustainably.

Target 2. By 2020, at the latest, biodiversity values have been integrated into national and local development and poverty reduction strategies and planning processes and are being incorporated into national accounting, as appropriate, and reporting systems.

Target 3. By 2020, at the latest, incentives, including subsidies, harmful to biodiversity are eliminated, phased out or reformed in order to minimize or avoid negative impacts, and positive incentives for the conservation and sustainable use of biodiversity are developed and applied, consistent and in harmony with the Convention and other relevant international obligations, taking into account national socioeconomic conditions.

Target 4. By 2020, at the latest, Governments, business and stakeholders at all levels have taken steps to achieve or have implemented plans for sustainable production and consumption and have kept the impacts of use of natural resources well within safe ecological limits.

Strategic Goal B

Reduce the Direct Pressures on Biodiversity and Promote Sustainable Use

Target 5. By 2020, the rate of loss of all natural habitats, including forests, is at least halved and where feasible brought close to zero, and degradation and fragmentation is significantly reduced.

Target 6. By 2020, all fish and invertebrate stocks and aquatic plants are managed and harvested sustainably, legally and applying ecosystem based approaches, so that overfishing is avoided, recovery plans and measures are in place for all depleted species, fisheries have no significant adverse impacts on threatened species and vulnerable ecosystems and the impacts of fisheries on stocks, species, and ecosystems are within safe ecological limits.

Target 7. By 2020, areas under agriculture, aquaculture and forestry are managed sustainably, ensuring conservation of biodiversity.

Target 8. By 2020, pollution, including from excess nutrients, has been brought to levels that are not detrimental to ecosystem function and biodiversity.

Target 9. By 2020, invasive alien species and pathways are identified and prioritized, priority species are controlled or eradicated, and measures are in place to manage pathways to prevent their introduction and establishment.

Target 10. By 2015, the multiple anthropogenic pressures on coral reefs, and other vulnerable ecosystems impacted by climate change or ocean acidification are minimized, so as to maintain their integrity and functioning.

Strategic Goal C

To Improve the Status of Biodiversity by Safeguarding Ecosystems, Species, and Genetic Diversity

Target 11. By 2020, at least 17% of terrestrial and inland water, and 10% of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes.

Target 12. By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained.

Target 13. By 2020, the genetic diversity of cultivated plants and farmed and domesticated animals and of wild relatives, including other socio-economically as well as culturally valuable species, is maintained, and strategies have been developed and implemented for minimizing genetic erosion and safeguarding their genetic diversity.

Strategic Goal D

Enhance the Benefits to All from Biodiversity and Ecosystem Services

Target 14. By 2020, ecosystems that provide essential services, including services related to water, and contribute to health, livelihoods, and well-being, are restored and safeguarded, taking into account the needs of women, indigenous and local communities, and the poor and vulnerable.

Target 15. By 2020, ecosystem resilience and the contribution of biodiversity to carbon stocks has been enhanced, through conservation and restoration, including restoration of at least 15% of degraded ecosystems, thereby contributing to climate change mitigation and adaptation and to combating desertification.

Target 16. By 2015, the Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization is in force and operational, consistent with national legislation.

Strategic Goal E

Enhance Implementation Through Participatory Planning, Knowledge Management and Capacity Building

Target 17. By 2015 each Party has developed, adopted as a policy instrument, and has commenced implementing an effective, participatory and updated national biodiversity strategy and action plan.

Target 18. By 2020, the traditional knowledge, innovations and practices of indigenous and local communities relevant for the conservation and sustainable use of biodiversity, and their customary use of biological resources, are respected, subject to national legislation and relevant international obligations, and fully integrated and reflected in the implementation of the Convention with the full and effective participation of indigenous and local communities, at all relevant levels.

Target 19. By 2020, knowledge, the science base and technologies relating to biodiversity, its values, functioning, status and trends, and the consequences of its loss, are improved, widely shared and transferred, and applied.

Target 20. By 2020, at the latest, the mobilization of financial resources for effectively implementing the Strategic Plan for Biodiversity 2011–2020 from all sources, and in accordance with the consolidated and agreed process in the Strategy for Resource Mobilization, should increase substantially from the current levels. This target will be subject to changes contingent to resource needs assessments to be developed and reported by Parties.

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