In the Light of Evolution: Volume II: Biodiversity and Extinction

DETAILS

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In the Light of Evolution

Volume II: Biodiversity and Extinction

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JOHN C. AVISE, STEPHEN P. HUBBELL,
and FRANCISCO J. AYALA, *Editors*

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Cover image: Stylized turtle, street art from Quito, Ecuador (artist unknown). Driven by human agriculture and industry, the Earth is currently undergoing the sixth mass extinction episode in its history. This image symbolizes both human industry and the countless unknown species that are disappearing before they can be catalogued and studied. Image courtesy of John C. Avise.

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Arthur M. Sackler, M.D.
1913-1987

Born in Brooklyn, New York, Arthur M. Sackler was educated in the arts, sciences, and humanities at New York University. These interests remained the focus of his life, as he became widely known as a scientist, art collector, and philanthropist, endowing institutions of learning and culture throughout the world.

He felt that his fundamental role was as a doctor, a vocation he decided upon at the age of four. After completing his internship and service as house physician at Lincoln Hospital in New York City, he became a resident in psychiatry at Creedmoor State Hospital. There, in the 1940s, he started research that resulted in more than 150 papers in neuroendocrinology, psychiatry, and experimental medicine. He considered his scientific research in the metabolic basis of schizophrenia his most significant contribution to science and served as editor of the *Journal of Clinical and Experimental Psychobiology* from 1950 to 1962. In 1960 he started publication of *Medical Tribune*, a weekly medical newspaper that reached over one million readers in 20 countries. He established the Laboratories for Therapeutic Research in 1938, a facility in New York for basic research that he directed until 1983.

As a generous benefactor to the causes of medicine and basic science, Arthur Sackler built and contributed to a wide range of scientific institutions: the Sackler School of Medicine established in 1972 at Tel Aviv University, Tel Aviv, Israel; the Sackler Institute of Graduate Biomedical Science at New York University, founded in 1980; the Arthur M. Sackler Science Center dedicated in 1985 at Clark University, Worcester, Massachusetts; and the Sackler School of Graduate Biomedical Sciences, established in 1980, and the Arthur M. Sackler Center for Health Communications, established in 1986, both at Tufts University, Boston, Massachusetts.

His pre-eminence in the art world is already legendary. According to his wife Jillian, one of his favorite relaxations was to visit museums and art galleries and pick out great pieces others had overlooked. His interest in art is reflected in his philanthropy; he endowed galleries at the Metropolitan Museum of Art and Princeton University, a museum at Harvard

University, and the Arthur M. Sackler Gallery of Asian Art in Washington, D.C. True to his oft-stated determination to create bridges between peoples, he offered to build a teaching museum in China, which Jillian made possible after his death, and in 1993 opened the Arthur M. Sackler Museum of Art and Archaeology at Peking University in Beijing.

In a world that often sees science and art as two separate cultures, Arthur Sackler saw them as inextricably related. In a speech given at the State University of New York at Stony Brook, *Some reflections on the arts, sciences and humanities*, a year before his death, he observed: ''Communication is, for me, the *primum movens* of all culture. In the arts . . . I find the emotional component most moving. In science, it is the intellectual content. Both are deeply interlinked in the humanities.'' The Arthur M. Sackler Colloquia at the National Academy of Sciences pay tribute to this faith in communication as the prime mover of knowledge and culture.

Contents

Preface to the *In the Light of Evolution* Series

Biodiversity—the genetic variety of life—is an exuberant product of the evolutionary past, a vast human-supportive resource (aesthetic, intellectual, and material) of the present, and a rich legacy to cherish and preserve for the future. Two urgent challenges, and opportunities, for 21st-century science are to gain deeper insights into the evolutionary processes that foster biotic diversity, and to translate that understanding into workable solutions for the regional and global crises that biodiversity currently faces. A grasp of evolutionary principles and processes is important in other societal arenas as well, such as education, medicine, sociology, and other applied fields including agriculture, pharmacology, and biotechnology. The ramifications of evolutionary thought also extend into learned realms traditionally reserved for philosophy and religion.

In 1973, Theodosius Dobzhansky penned a short commentary entitled "Nothing in biology makes sense except in the light of evolution." Most scientists agree that evolution provides the unifying framework for interpreting biological phenomena that otherwise can often seem unrelated and perhaps unintelligible. Given the central position of evolutionary thought in biology, it is sadly ironic that evolutionary perspectives outside the sciences have often been neglected, misunderstood, or purposefully misrepresented.

The central goal of the *In the Light of Evolution (ILE)* series is to promote the evolutionary sciences through state-of-the-art colloquia—in the series of Arthur M. Sackler colloquia sponsored by the National Academy of Sciences—and their published proceedings. Each installment explores evolutionary perspectives on a particular biological topic that is scientifically intriguing but also has special relevance to contemporary societal issues or challenges. Individually and collectively, the *ILE* series aims to interpret phenomena in various areas of biology through the lens of evolution, address some of the most intellectually engaging as well as pragmatically important societal issues of our times, and foster a greater appreciation of evolutionary biology as a consolidating foundation for the life sciences.

The organizers and founding editors of this effort (Avise and Ayala) are the academic grandson and son, respectively, of Theodosius Dobzhansky, to whose fond memory this *ILE* series is dedicated. May Dobzhansky's words and insights continue to inspire rational scientific inquiry into nature's marvelous operations.

John C. Avise and Francisco J. Ayala
Department of Ecology and Evolutionary Biology,
University of California, Irvine (January 2007)

Preface to *In the Light of Evolution, Volume II: Biodiversity and Extinction*

The Earth's biodiversity is a wellspring for scientific curiosity about nature's workings. It is also a source of joy and inspiration for inquisitive minds, from poets to philosophers, and provides life-support services. According to Kellert (2005), biodiversity affords humanity nine principal types of benefit: utilitarian (direct economic value of nature's goods and services), scientific (biological insights), aesthetic (inspiration from nature's beauty), humanistic (feelings deeply rooted in our inherent attachment to other species), dominionistic (physical and mental well-being promoted by some kinds of interactions with nature), moralistic (including spiritual uplifting), naturalistic (curiosity-driven satisfaction from the living world), symbolic (nature-stimulated imagination, communication, and thought), and even negativistic (fears and anxieties about nature, which can actually enrich people's life experience). Whether or not this list properly characterizes nature's benefits, the fact is that a world diminished in biodiversity would be greatly impoverished.

Many scientists have argued that as a consequence of human activities the Earth has entered the sixth mass extinction episode (and the only such event precipitated by a biotic agent) in its 4-billion-year history (Leakey and Lewin, 1995; Glavin, 2007). The last catastrophic extinction, which occurred about 65 million years ago and was the *coup-de-grace* for nonavian dinosaurs, marine ammonites, and many other evolutionary lineages, happened rather suddenly after a large asteroid slammed into the planet. Today, most of the biotic holocaust is due—directly or indirectly—to local, regional, and global environmental impacts from a burgeoning human population. The first phase of the current extinction episode started about 50,000 to 100,000 years ago when modern humans began dispersing around the planet. The second phase started 10,000 years ago with further population increases and land-use changes associated with the invention of agriculture. A third phase of environmental alteration and biodiversity loss was ushered in by the Industrial Revolution. E. O. Wilson (1992) estimated that the Earth is currently losing approximately 0.25% of its remaining species per year (such that at least 12,000 species may be going extinct annually). Such estimates are educated guesses because they represent extrapolations (from species–area curves and other evidence) to taxa that undoubtedly are disappearing even before they can be identified and studied. Nevertheless, they do reveal the general magnitude of the ongoing extinction crisis. For many species that manage to avoid extirpation, local and regional populations are being decimated.

The modern extinction crisis is prompting scientific efforts on many fronts. Systematists are striving to describe biodiversity and reconstruct the Tree of Life. Ecologists are mapping the distributions of biodiversity and global hotspots that merit special conservation attention. Paleontologists are placing the current crisis in temporal context with regard to the Earth's long geological history, and also to the recent history of human impacts on biodiversity across timescales ranging from decades to millennia. Educators and concerned scientists are striving to alert government leaders, policymakers, and the public to the biodiversity crisis. Conservation efforts (including those by many nongovernment organizations) are underway to slow the pace of biological extinctions. However, unless conservation achievements accelerate quickly, the outlook for biodiversity in and beyond the 21st century remains grim.

This book is the outgrowth of the Arthur M. Sackler Colloquium on "Biodiversity and Extinction," which was sponsored by the National Academy of Sciences on December 7–8, 2007, at the Academy's Arnold and Mabel Beckman Center in Irvine, California. It is the second in a series of colloquia under the umbrella title "In the Light of Evolution." The first book in this series was titled *In the Light of Evolution, Volume I: Adaptation and Complex Design* (Avise and Ayala, 2007).

The chapters that follow illustrate current scientific perspectives on biodiversity and extinction across varied timescales and diverse taxonomic groups. Chapters are arranged in four parts, each immediately preceded by a brief editorial introduction. Authors in Part I address contemporary patterns of biodiversity and extinction in animals representing several imperiled taxa and environmental settings, and authors in Part II do likewise for various modern plants and microbes. In Part III, authors add historical perspective by addressing biodiversity trends and extinction processes in the near and distant paleontological past. Authors in Part

IV offer their projections for the future of biodiversity given the pace of environmental alteration by human activities. Collectively, the chapters in this book synthesize recent scientific information and ideas about the abundance and threats to biodiversity in the past, present, and projected future.

The current extinction crisis is of human making, and any favorable resolution of that biodiversity crisis—among the most dire in the 4-billion-year history of the Earth—will have to be initiated by mankind. Little time remains for the public, corporations, and governments to awaken to the magnitude of what is at stake. Preserving biodiversity is undeniably in humanity's enlightened self-interest, but the tragic irony is that a majority of humanity is not yet enlightened to this fact. It is hoped that the information and sentiments in this book will assist that critical educational mission.

Part I

CONTEMPORARY PATTERNS AND PROCESSES IN ANIMALS

There is no doubt that humans are the root cause of most ecosystem stresses and biotic extinctions in the modern world. Negative human pressures on biodiversity occur via pollution, introductions of alien species, overexploitation, landscape transformations, and other factors. Like the asteroid impact 65 million years ago, human impacts extend to many kinds of terrestrial, aquatic, and marine organisms. The chapters in Part I illustrate some of the challenges of quantifying the magnitude of extant biodiversity and deciphering extinction rates and patterns in a diverse but representative selection of contemporary animal taxa.

Oceans cover three-quarters of the Earth's surface, and their inhabitants might seem at first thought to be somewhat buffered (compared to terrestrial and freshwater species) against anthropogenic disturbance. However, in Chapter 1, Jeremy Jackson compiles evidence from four major marine realms—estuaries and coastal areas, continental shelves, open ocean pelagic zone, and coral reefs—that marine ecosystems are under extreme duress from the oft-synergistic effects of habitat destruction, overfishing, introduced species, warming and acidification, toxins, and nutrient runoff. One common result has been the degradation of biodiverse marine ecosystems with complex food webs capped by an abundance of top-echelon predators into simplified biotic communities increasingly dominated by smaller animals, algae, and microbes. Among the many ramifications have been the economic collapse of numerous marine fisheries and massive degradation of coral reefs that formerly rivaled tropical rainforests in terms of spatial coverage and biotic richness.

The data paint a disturbing picture about current and projected ecological states for the world's oceans.

In Chapter 2, David Wake and Vance Vredenburg describe a similarly gloomy scenario for the global status of amphibians. Of the approximately 6,300 extant species of frogs, salamanders, and caecilians, at least one-third are currently threatened with extinction, and many more are likely to become so in the near future. A dramatic worldwide decline in amphibian populations was first noticed in the late 1980s. Several ecological factors including habitat degradation and climatic changes probably are involved, but so too is an unanticipated, recently uncovered threat: an emerging virulent disease (chytridiomycosis) caused by a pathogenic fungus. The source of this fungus and its mode of spread are poorly understood, but the disease (perhaps in synergy with other ecological factors) has devastated amphibian populations in such distant sites as the Americas and tropical Australia. Whatever the proximate and ultimate causes of the ongoing amphibian extinctions, the trend is especially disturbing because amphibians otherwise have been quintessential evolutionary survivors that managed to persist across several earlier mass extinction events in the Earth's history.

Biodiverse coral reefs are among the most threatened ecological systems on Earth. About 70% of coral reefs globally have either been degraded beyond recognition in recent years (20%), are in imminent danger of collapse (24%), or are under longer term threat of demise (26%) (Wilkinson, 2004). In Chapter 3, Marjorie Reaka and colleagues survey reef-dwelling stomatopods (a large group of marine crustaceans) as a model taxon to assess global hotspots of extant biodiversity, endemism, and extinction risk, the intent being to identify evolutionary sources and sinks of stomatopod diversity, infer driving mechanisms, and provide an additional focus for conservation and management efforts on coral reefs. Stomatopod species diversity (like that of several other reef-dwelling marine taxa) is highest in the Indo-Australian Archipelago, gradually declines eastward across the central Pacific, and shows a secondary peak of species richness in the southwestern Indian Ocean. From these and other data (related to body size, ecology, and spatial pattern of endemism), the authors explain how a "merry-go-round" evolutionary model might account for the differential dynamics of species origin and extinction in different ocean regions.

Extinctions in the ongoing biodiversity crisis apply not only to free-living organisms but also to their parasites. In Chapter 4, Andy Dobson and colleagues address the possible magnitude of this problem by reviewing estimates of the total number of parasitic species on Earth (with special reference to helminthes that parasitize vertebrate animals) and the fraction of extant biodiversity that is parasitic. The authors conclude that about 10–15% of parasitic helminthes (Trematoda, Cestoda, Acanthocephala, Nematoda) are at risk of extinction by virtue of being dependent on threatened or endangered species of vertebrate host. They also conclude that parasite species diversity does not map linearly onto host species diversity, and that approximately three-quarters of all links in food webs involve a parasitic species. These findings provide a sobering reminder that the current extinction pulse is affecting many kinds of organisms (not just the conspicuous megafauna), and that extinction processes could therefore have many unforeseen ramifications for ecosystem operations.

1

Ecological Extinction and Evolution in the Brave New Ocean

JEREMY B. C. JACKSON

The great mass extinctions of the fossil record were a major creative force that provided entirely new kinds of opportunities for the subsequent explosive evolution and diversification of surviving clades. Today, the synergistic effects of human impacts are laying the groundwork for a comparably great Anthropocene mass extinction in the oceans with unknown ecological and evolutionary consequences. Synergistic effects of habitat destruction, overfishing, introduced species, warming, acidification, toxins, and massive runoff of nutrients are transforming once complex ecosystems like coral reefs and kelp forests into monotonous level bottoms, transforming clear and productive coastal seas into anoxic dead zones, and transforming complex food webs topped by big animals into simplified, microbially dominated ecosystems with boom and bust cycles of toxic dinoflagellate blooms, jellyfish, and disease. Rates of change are increasingly fast and nonlinear with sudden phase shifts to novel alternative community states. We can only guess at the kinds of organisms that will benefit from this mayhem that is radically altering the selective seascape far beyond the consequences of fishing or warming alone. The prospects are especially bleak for animals and plants compared

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with metabolically flexible microbes and algae. Halting and ultimately reversing these trends will require rapid and fundamental changes in fisheries, agricultural practice, and the emissions of greenhouse gases on a global scale.

About 10 years ago, several of us concluded that the global ecological condition of the oceans because of overfishing was as dire as that of tropical rain forests, and that future losses would be enormous and potentially irreversible if action were not taken promptly to reverse the trajectories of decline (Pauly *et al.*, 1998; Jackson *et al.*, 2001; Christensen *et al.*, 2003; Myers and Worm, 2003). The scientific response was chilly, as evidenced by the statement of task for the recent National Research Council (NRC) report on the dynamics of marine ecosystems (NRC, 2006), which refers to our work in terms that emphasize the "high profile" of the articles (as if this were unseemly), the unconventional (and therefore suspect) nature of the data, and our assertions about the importance of shifting baselines and fishing down marine food webs, and that 90% of large predatory fish stocks are gone. In the end, the NRC report cautiously confirmed the conclusions it was convened to evaluate. But many scientists remain skeptical, apparently because (*i*) most conclusions are necessarily based on patterns and correlations using data gathered for many different purposes rather than experiments, (*ii*) the traditional emphasis in biological oceanography on bottom-up nutrient forcing rather than top-down control by predators, and (*iii*) the strong implication that most fisheries have been mismanaged for decades.

The focus of the NRC report (2006) was on fishing, but the problems are vastly greater because of the additional effects on marine ecosystems of biological, toxic, and nutrient pollution, habitat loss, global climate change, and the synergies among all of these different drivers of ecological change (Jackson *et al.*, 2001; Knowlton, 2001; Riebesell, 2004; Pandolfi *et al.*, 2005; Schmittner, 2005; Rabalais *et al.*, 2007). There is also considerable uncertainty about the relative importance and interactions among local perturbations, such as fishing and pollution, versus global changes in climate and ocean chemistry that operate over very different and noncongruent temporal and spatial scales (Hoegh-Guldberg *et al.*, 2007; Knowlton and Jackson, 2008). Trophic structure and biodiversity are also key components of the resistance and resilience of marine ecosystems to future perturbations (Bascompte *et al.*, 2005; Worm *et al.*, 2006), but we are only beginning to document how these parameters change across a broad spectrum of human and natural disturbance. The problems are complex because of the huge numbers of species and different kinds of perturbations involved, the nonlinear dynamics of interactions among them, and the infancy of the emerging theoretical framework required to interpret the results (Knowlton, 1992; Scheffer *et al.*, 2001; Hsieh *et al.*, 2005).

Much new data and analyses have appeared in the last 5 years, sometimes with sharply conflicting interpretations, about the magnitude and rates of change in abundance of particular species. Regardless of these uncertainties, however, it is increasingly apparent that all of the different kinds of data and methods of analysis point in the same direction of drastic and increasingly rapid degradation of marine ecosystems. Here, I examine some of the most important of these new results since the publication of my previous synthesis (Jackson *et al.*, 2001), with emphasis on coastal seas and estuaries, continental shelves, the open ocean pelagic realm, and coral reefs, about which I am most familiar. The biology and substantial threats to the ecology of the deep sea have been recently reviewed by Koslow (2007) and are not considered here. I then discuss what I believe will be the future of marine ecosystems if the drivers of change continue unabated, and address the kinds of changes in patterns of consumption and energy use that will be required to turn the situation around.

ESTUARIES AND COASTAL SEAS

People have congregated along the coast from the beginnings of humanity, and the cumulative effects of exploitation, habitat destruction, and pollution are more severe in estuaries and coastal seas than anywhere else in the ocean except for coral reefs.

Bay of Fundy

New detailed studies of the Quoddy region of the Bay of Fundy (Lötze and Milewski, 2004) and the Wadden Sea (Lötze, 2005; Lötze *et al.*, 2005) confirm and refine conclusions developed earlier based primarily on studies of Chesapeake Bay and Pamlico Sound (Jackson, 2001; Jackson *et al.*, 2001). The Bay of Fundy is particularly interesting because ecological degradation is so great despite comparatively good water quality compared with most other estuaries (Lötze, 2005; Lötze *et al.*, 2006). Exploitation began with whaling and hunting and fishing of other marine mammals, birds, and cod. The 16 original mammal species present before European contact were hunted to very low levels by 1900, with 3 extinct species including the sea mink *Mustela macrodon*, Atlantic walrus *Odobenus rosmarus rosmarus*, and possibly the coastal northwest Atlantic gray whale *Eschrichtius robustus*, as well as 7 more species that were severely reduced (Lötze and Milewski, 2004). Subsequent protection resulted in strong recovery of pinnepeds, but whales have not recovered, including the northern right whale, which has declined from an estimated population of 10,000–15,000 in the northwest Atlantic to a mere 300 individuals. Among the 83 species of birds from the region, 40% have declined severely, including 3 species that were locally extirpated and another 3 hunted to extinction. Salmon were heavily exploited before records began, but even the stocks remaining in 1890–1900 were reduced by a further 99.5% by the end of the 20th century. The big three marine groundfish—cod, pollock, and haddock—were severely reduced before 1900, as elsewhere (Lötze and Milewski, 2004; Rosenberg *et al.*, 2005), and catches were further reduced to just 3–37% of 1900 values by 2000. At the same time, several noncommercial species increased greatly in abundance. By the time scientific surveys began in 1970, groundfish were being rapidly replaced by shellfish and seaweeds as the major fisheries that are now also in decline (Lötze and Milewski, 2004).

Global Patterns of Exploitation

Suggestions that we had somehow focused on only the worst-case scenarios in our article on overfishing (Jackson *et al.*, 2001) were addressed by an exhaustive review of 12 coastal seas and estuaries worldwide for which extensive archeological, historical, and early scientific data were available (Lötze *et al.*, 2006). We examined ≈80 species or species groups that were assigned to six major taxonomic groups and seven ecological guilds. Average global degradation ranged from a low of 39% for crustaceans to 91% for oysters (Table 1.1). Levels of overall degradation for all major taxo-

TABLE 1.1 Percent Decline (Biomass, Catch, Percent Cover) for Fauna and Flora from Various Marine Environments

Taxon	Starting Date	Location	% Loss	Ref.
Estuaries and coastal seas				
Large whales	Pristine	Global	85	Lötze *et al.* (2006)
Small whales	Pristine	Global	59	Lötze *et al.* (2006)
Pinnipeds and otters	Pristine	Global	55	Lötze *et al.* (2006)
Sirenia	Pristine	Global	90	Lötze *et al.* (2006)
Raptors	Pristine	Global	79	Lötze *et al.* (2006)
Seabirds	Pristine	Global	57	Lötze *et al.* (2006)
Shorebirds	Pristine	Global	61	Lötze *et al.* (2006)
Waterfowl/waders	Pristine	Global	58	Lötze *et al.* (2006)
Sea turtles	Pristine	Global	87	Lötze *et al.* (2006)
Diadromous fish	Pristine	Global	81	Lötze *et al.* (2006)
Groundfish	Pristine	Global	62	Lötze *et al.* (2006)
Large pelagics	Pristine	Global	74	Lötze *et al.* (2006)
Small pelagics	Pristine	Global	45	Lötze *et al.* (2006)

TABLE 1.1 Continued

Taxon	Starting Date	Location	% Loss	Ref.
Oysters	Pristine	Global	91	Lötze *et al.* (2006)
Mussels	Pristine	Global	47	Lötze *et al.* (2006)
Crustaceans	Pristine	Global	39	Lötze *et al.* (2006)
Other invertebrates	Pristine	Global	49	Lötze *et al.* (2006)
Seagrass	Pristine	Global	65	Lötze *et al.* (2006)
SAV[a]	Pristine	Global	48	Lötze *et al.* (2006)
Wetlands	Pristine	Global	67	Lötze *et al.* (2006)
Large carnivores	Pristine	Global	77	Lötze *et al.* (2006)
Small carnivores	Pristine	Global	60	Lötze *et al.* (2006)
Large herbivores	Pristine	Global	63	Lötze *et al.* (2006)
Small herbivores	Pristine	Global	54	Lötze *et al.* (2006)
Suspension feeders	Pristine	Global	68	Lötze *et al.* (2006)
Shelf and pelagic fisheries				
Large predatory fishes	1900	N. Atlantic	89	Christensen *et al.* (2003)
Atlantic cod	1852	Scotian shelf	96	Rosenberg *et al.* (2005)
Fish 4–16 kg	Pristine	North Sea	97	Jennings and Blanchard (2004)
Fish 16–66 kg	Pristine	North Sea	99	Jennings and Blanchard (2004)
Large predatory fish	1950s	Global	90	Myers and Worm (2003)
Large pelagic predators	1950s	Tropical Pacific	90	Polacheck (2006)
Fishery biomass	1959	Bohai Sea	95	Tang *et al.* (2003)
Coastal and pelagic sharks				
Hammerheads	1986	N.W. Atlantic	89	Baum *et al.* (2003)
Scalloped hammerhead	1972	North Carolina	98	Myers *et al.* (2007)
White	1986	N.W. Atlantic	79	Baum *et al.* (2003)
Tiger	1986	N.W. Atlantic	65	Baum *et al.* (2003)
Tiger	1973	North Carolina	97	Myers *et al.* (2007)
Carcharhinus spp.	1986	N.W. Atlantic	61	Baum *et al.* (2003)
Thresher	1986	N.W. Atlantic	80	Baum *et al.* (2003)
Blue	1986	N.W. Atlantic	60	Baum *et al.* (2003)
Mako	1986	N.W. Atlantic	70	Baum *et al.* (2003)
Mako	1950s	Gulf of Mexico	45	Baum and Myers (2004)
Oceanic whitetip	1950s	Gulf of Mexico	99	Baum and Myers (2004)
Silky	1950s	Gulf of Mexico	91	Baum and Myers (2004)
Dusky	1950s	Gulf of Mexico	79	Baum and Myers (2004)
Dusky	1972	North Carolina	99	Myers *et al.* (2007)
Blacktip shark	1972	North Carolina	93	Myers *et al.* (2007)

Continued

TABLE 1.1 Continued

Taxon	Starting Date	Location	% Loss	Ref.
Bull shark	1973	North Carolina	99	Myers *et al.* (2007)
Sandbar shark	1976	North Carolina	87	Myers *et al.* (2007)
Coral reefs				
Live coral cover	1977	Caribbean	80	Newman *et al.* (2006)
Live coral cover	1977	Caribbean	93	Gardner *et al.* (2003)
Live coral cover	1980–1982	Indo-West Pacific	46	Pandolfi and Jackson (2006)
Commercial sponges	1924	Florida	89	Lessios *et al.* (1984)
Diadema antillarum	1977	Caribbean	92	Aronson and Precht (2001)
Reef fish density	1977	Caribbean	90	Gardner *et al.* (2003)
Green turtle	1700s	Caribbean	>99	McClenachan and Cooper (2008)
Hawksbill turtle	1700s	Caribbean	>99	McClenachan and Cooper (2008)
Goliath grouper	1956	Florida Keys	96	McClenachan *et al.* (2007)
Large carnivores	Pristine	Global	85	Lewis (2002); Pandolfi *et al.* (2005)
Small carnivores	Pristine	Global	61	Lewis (2002); Pandolfi *et al.* (2005)
Large herbivores	Pristine	Global	87	Lewis (2002); Pandolfi *et al.* (2005)
Small herbivores	Pristine	Global	66	Lewis (2002); Pandolfi *et al.* (2005)
Corals	Pristine	Global	61	Lewis (2002); Pandolfi *et al.* (2005)
Suspension feeders	Pristine	Global	49	Lewis (2002); Pandolfi *et al.* (2005)
Seagrasses	Pristine	Global	50	Lewis (2002); Pandolfi *et al.* (2005)

NOTES: Starting dates are beginning of time series except in cases of estimated declines from the pristine, unexploited condition. See original references for details.

[a] Submerged aquatic vegetation.

nomic groups combined based on multivariate ordination varied roughly 2-fold among the 12 regions, from ≈43% in the Bay of Fundy to 74% in the Adriatic, but the trajectories and patterns of degradation were strikingly similar for all of them (Lötze *et al.*, 2006). Most of the mammals, birds, and reptiles were severely depleted by 1900 and had declined even further by 1950. Among fish, diadromous salmon and sturgeon were depleted first, and then groundfish and large pelagics like tuna and sharks, and finally small pelagics like herring, menhaden, and sardines.

Oysters were the first invertebrates to suffer extreme depletion, and the massive destruction of oyster reefs by dredging has permanently destroyed much of the formerly great habitat complexity of estuaries and coastal seas worldwide (Jackson *et al.*, 2001; Kirby, 2004; Lötze *et al.*, 2006). Depletion of oysters moved progressively farther and farther from major markets like New York City, San Francisco, and Sydney, until eventually all of the stocks along eastern and western North America and eastern Australia had collapsed (Kirby, 2004). None of these wild stocks have substantially recovered because of eutrophication, disease, and habitat loss as described below, and oyster production now depends almost entirely on aquaculture.

Today, most fish and invertebrate stocks are severely depleted globally, and one-half to two-thirds of global wetlands and seagrass beds also have been lost (Table 1.1). Of the 80 species surveyed, 91% are depleted, 31% are rare, and 7% are extinct (Kirby, 2004). Nowhere are there any substantial signs of recovery, despite belated conservation efforts, except for nominal increases in some highly protected birds and mammals.

Patterns of Biological and Chemical Pollution

Beginning in the 1950s, accelerating increases in the number of introduced species and degradation of water quality due to excess nutrients from the land have surpassed fishing as the major factors in the degradation of estuaries and coastal seas, although fishing still plays a major role (Jackson, 2001; Jackson *et al.*, 2001). Numbers of introduced species in the five best-studied estuaries range from 80 to 164 (average 117) species, where they have commonly displaced native animals and plants to become the dominant species. Geochemical and paleobotanical evidence of eutrophication in cores is readily apparent since at least the 19th century due to deforestation and agriculture, with consequent runoff of sediments and nutrients (Zimmermann and Canuel, 2002; Colman and Bratton, 2003; Lötze *et al.*, 2006). These effects were aggravated by the extirpation of suspension feeders like oysters and menhaden (Jackson, 2001; Jackson *et al.*, 2001). The situation then largely stabilized until about 1950 when new influxes of nitrogen fertilizers began. Today, most of the estuaries experience massive nutrient inputs, extended summer eutrophication and hypoxia, and population explosions of microbes (Diaz, 2001; Jackson *et al.*, 2001).

Synergistic Effects

The degrading effects of fishing, habitat destruction, introduced species, and eutrophication reinforce each other through positive feedbacks (Jackson, 2001; Jackson *et al.*, 2001; Lötze *et al.*, 2006). For example, oysters were nearly eliminated by overfishing, but their recovery is now hampered by hypoxia due to eutrophication, by introduced species that compete for space and cause disease, and by the explosive rise of formerly uncommon predators that were previously kept in check by now overfished species (Lenihan and Peterson, 1998; Myers *et al.*, 2007). Much of the overall decline of the 80 species reviewed by Lötze *et al.* (2006) was due to multiple suites of drivers: 45% of depletions and 42% of extinctions involved multiple impacts. Nowhere have these drivers been brought under effective regulation or control.

CONTINENTAL SHELVES

Ecological degradation on continental shelves is almost as severe as in estuaries and coastal seas, and the drivers are similar, albeit in somewhat different proportions.

Exploitation

Longline fishing and trawling have removed 89% of the pristine abundance of prized large predatory fishes like cod, pollock, and haddock in the North Atlantic in the last 100 years, and cod have been depleted by 96% since 1852 (Table 1.1) (Christensen *et al.*, 2003; Rosenberg *et al.*, 2005). The effects on sharks have also been enormous (Table 1.1). Large sharks most commonly caught by pelagic longlines in the northwest Atlantic were reduced by 40–89% between 1986 and 2000 (Baum *et al.*, 2003). Likewise, in the Gulf of Mexico, longline fishing and trawling reduced the four commonest large pelagic species by 45–99% in the 40 years between the 1950s and 1990s (Baum and Myers, 2004). Small coastal sharks in the Gulf of Mexico have also been severely reduced, except for some species that have experienced release from predation by the overfishing of their predators (Shepherd and Myers, 2005). Of the 23 species for which adequate data were available, 16 species declined between 1972 and 2002, and the declines were statistically significant for 9 species, 3 of which were reduced to <2% of their 1972 abundance. Seven species also increased, 3 of them significantly, including the smooth dogfish, which increased 13-fold. However, these were deepwater species generally out of reach of trawling.

Release from predators can have spectacular consequences through the development of trophic cascades. For example, reductions of ≈90–99% for 11 large sharks that consume smaller elasmobranchs along the northwest Atlantic Coast of North America resulted in the increase of 12 of their 14 common prey species (Myers *et al.*, 2007). Populations of one of these smaller species, the cownose ray *Rhinoptera bonasus*, exploded to some 40 million. Each ray can consume ≈210 g shell-free wet weight of bivalve mollusks per day, assuming that they are available. The rays migrate through Chesapeake Bay each year, where they stay for ≈100 days, which amounts to a potential consumption of 840,000 metric tons of mollusks/year. In contrast, the commercial harvest of bay scallops that peaked in the early 1980s had fallen by 2003 to only 300 metric tons. Thus, the rays could potentially consume 2,500 times the commercial harvest, and it is hardly surprising that the once prosperous clam fisheries have totally collapsed.

The canonical example of a trophic cascade involves the near extinction of sea otters by hunting in the northeast Pacific that resulted in explosions of sea urchins that in turn eliminated entire kelp forests by overgrazing (Estes and Duggins, 1995). Trophic cascades have also been documented for the formerly cod-dominated ecosystem of the northwest Atlantic (Frank *et al.*, 2005), where removal of large groundfish resulted in large increases in pelagic shrimp and snow crabs, decreases in large zooplankton, and increases in phytoplankton. Thus, removal of top-down controls affects ecosystem structure and function of large marine ecosystems with complex food webs, as well as simpler, low-diversity systems.

The occurrence of trophic cascades is closely linked to the phenomenon of fishing down the food web (Pauly *et al.*, 1998). Analysis of Food and Agriculture Organization global fisheries data showed a decline in mean trophic level of the global predatory fish catch of ≈0.1 per decade since 1950. There has been much discussion of the quality and suitability of the data, and whether the decline in trophic level primarily reflects serial depletion of overfished species or serial additions of lower trophic level species caused by a depletion of their predators (Essington *et al.*, 2006; NRC, 2006). Regardless of the relative importance of these different mechanisms, however, there is increasingly reliable evidence for the pervasive decline in mean trophic level in heavily fished ecosystems. For example, mean trophic level fell from 4.06 to 3.41 in the Bohai Sea between 1959 and 1998 (Zhang *et al.*, 2007), a decline of 0.16–0.19 per decade. This drop parallels a dramatic 95% decline in total fish catch from 190 to 10 kg per standardized haul per hour (Table 1.1) and a precipitous drop in the proportion of piscivorous fish in the standardized hauls from 29.3% to 0% of the catch (Tang *et al.*, 2003). In contrast, planktivorous species increased from 4.75% to 58.0% of the catch in the same hauls.

Finally, Jennings and Blanchard (2004) used the theoretical abundance–body mass relationship derived from macroecological theory to estimate the pristine biomass of fishes in the North Sea in comparison with the size and trophic structure of heavily exploited populations in 2001. The estimated total biomass of all fishes 64 g to 64 kg declined 38% while the mean turnover time of the population was estimated to have dropped from 3.5 to 1.9 years. Large fishes 4–16 kg were estimated to have declined by 97.4%, and species 16–66 kg were estimated to have declined by 99.2%. The great importance of these calculations is that they are entirely independent of all of the assumptions and controversies surrounding fisheries catch data and models, and yet lead to predictions entirely consistent with the most extreme estimates of fishery declines.

Habitat Destruction by Trawling and Dredging

Trawling reduces the three-dimensional structure and complexity of sea floor habitats to bare sediment; reduces the size, biological diversity, and turnover time of dominant species; and results in entirely new associations of species that may persist for decades even if trawling is halted

FIGURE 1.1 Impact of trawling on the seafloor at ≈18 m depth in the Swan Island Conservation Area, northern Gulf of Maine (Auster, 1998). The straight lines are furrows made by the trawl, and the debris is polychaete worm tubes.

(Fig. 1.1) (Dayton *et al.*, 1995; Auster, 1998; NRC, 2002). The magnitude of effects increases with the frequency and geographic scale of trawling. The most striking data are from New England and the Gulf of Mexico (NRC, 2002), although the situation is almost certainly comparable on continental shelves around the world (Dayton *et al.*, 1995). In New England, the total area fished (TAF) by trawling is 138,000 km^2, and 56% of the sample areas are fished more than once a year, so that the equivalent of 115% of the TAF is fished every year. In the Gulf of Mexico, the TAF is 270,000 km^2, 57% of the sample areas are fished more than once a year, and trawls sweep 255% of the TAF each year. Thus, trawling has drastically degraded most of the sea floor in these huge regions, and with multiple trawling episodes per year at favored sites, there is obviously no opportunity for ecosystem recovery.

Eutrophication, Dead Zones, and the Rise of Slime

Nutrient runoff is naturally greatest, and eutrophication, hypoxia, and toxic blooms are most intense, in estuaries and coastal seas like the Adriatic and Baltic seas and Chesapeake and San Francisco bays (Diaz, 2001; Jackson, 2001; Jackson *et al.*, 2001; Lötze *et al.*, 2006). However, major river systems like the Amazon, Yangtze, and Mississippi–Missouri also discharge vast amounts of nutrients, sediments, and organic matter into relatively small areas of open coast and surrounding continental shelves. The enormous increase in the use of chemical fertilizers in the drainage basins of these great rivers over the past 50 years (Tilman *et al.*, 2002), coupled with the virtual elimination of suspension feeding oysters and wetlands along their delta margins, has resulted in the formation of vast eutrophic and hypoxic regions comparable with the worst conditions in estuaries (Diaz, 2001).

The iconic American example is the hypoxic "dead zone" that extends some 500 km west of the Mississippi delta. The area of the hypoxic zone has doubled in the past 20 years to ≈20,000 km^2, and the rate of increase in area is a linear function of nitrogen loading from the Mississippi drainage (Fig. 1.2) (Rabalais *et al.*, 2007; Turner *et al.*, 2008). Analyses of the geochemistry and mineralogy of cores shows that hypoxic conditions were uncommon before the 1950s, strongly supporting the hypothesis that their formation is due to comparatively recent human impacts and is not a natural phenomenon. The dead zone expands during the summer, when hypoxia extends from shallow depths to the sea floor, and there is mass mortality of most animals that cannot swim away, including major fisheries species like shrimp. The dead zone is hardly dead, however, but supports an extraordinary biomass of diverse microbes and jellyfish that may constitute the only surviving commercial fishery. In addition,

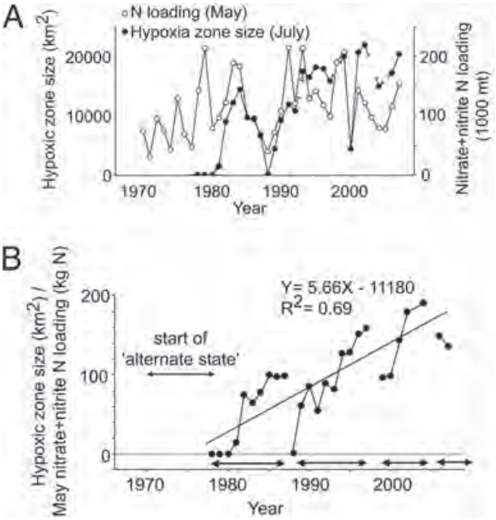

FIGURE 1.2 Hypoxia and nitrogen loading in the Gulf of Mexico (Turner *et al.*, 2008). (*A*) Annual variations in the size of the hypoxic zone in late July and the nitrate plus nitrite nitrogen loading for the preceding May. (*B*) Increase in the ratio of the size of the hypoxic zone relative to nitrogen loading the preceding year. The breaks in the curve reflect hurricanes and droughts, but the overall trend is highly significant.

and extending beyond the dead zone, toxic blooms of dinoflagellates like *Karenia brevis* occur over areas as large as the entire northwestern Gulf of Mexico.

THE OPEN OCEAN PELAGIC REALM

Myers and Worm (2003) fired a shot heard around the world when they published their controversial assertion that 90% of all of the large (average approximately ≥50 kg), open ocean tuna, billfishes, and sharks in the ocean were gone. Severe depletion of coastal and shelf fisheries was widely accepted, but the open ocean was still considered one of the last great wild places on Earth.

Exploitation

Much of the controversy revolves around the use or misuse of highly complex "state-of-the-art stock assessment methods" (Sibert *et al.*, 2006) to estimate fisheries impacts on population biomass, size, and trophic status of top-level predators that are beyond the ability of most ecologists to evaluate. There has also been a great deal of name-calling, such as referring to Myers's and Worm's calculations as "folly" and "fantasy" (Walters, 2003), and outrage about the publicity that their article received from the press (Polacheck, 2006). Nevertheless, the NRC report acknowledged declines in the range of 65–80% (NRC, 2006) that are much greater than anyone was admitting to before Myers's and Worm's article was published.

Ward and Myers (2005) subsequently evaluated the status of 19 oceanic fisheries species in the central Tropical Pacific between the 1950s and the 1990s using scientific survey and official observer data. There were 12 species of large predatory sharks, tunas, and billfishes and 7 smaller species <17 kg. All 12 large predators showed significant declines in biomass, and 11 of the 12 species decreased in average body mass by 29–73%, whereas 5 of 7 smaller species showed no significant change and skipjack tuna significantly increased (Ward and Myers, 2005). Moreover, the pelagic stingray *Dasyatis violacea* and pomfrets, which were absent in the 1950s, appeared in even greater abundance than any of the original smaller species. Overall, biomass declined 89.7% and large predators declined by 90.3%—the same as the declines originally reported by Myers and Worm (2003). Perhaps more important than the actual magnitude of decline, however, is the clear shift in species composition and relative abundance in the pelagic community reminiscent of the increase in mesopredators in the northwest Atlantic and Gulf of Mexico (Shepherd and Myers, 2005; Myers *et al.*, 2007). Pelagic fisheries are a vast uncontrolled experiment whose ecosystem consequences are still unknown. Nevertheless, Ward's and Myers's results clearly point toward the potential for strong trophic cascades and significant declines in mean trophic level as fishing erodes top-down control.

Climate Change

Warming and acidification of the pelagic realm due to the rise of CO_2 comprise another uncontrolled experiment on a global scale (Feely *et al.*, 2004). Sea-surface warming increases the stratification of the oceans because warmer and lighter surface waters inhibit upwelling of cooler and denser nutrient-rich waters from below (Schmittner, 2005). Increased stratification may have already caused the drop in productivity in the northern Pacific that is widely described by biologists as a "regime shift" in the composition of open-ocean plankton communities (McGowan *et al.*, 2003). Moreover, climate models suggest that the oceans may move into a permanent El Niño condition (Wara *et al.*, 2005; Fedorov *et al.*, 2006). Uncertainties abound regarding the degree to which upwelling could be permanently suppressed, but if ocean productivity declines, there will be an inevitable further decline in fisheries (McGowan *et al.*, 2003; Field *et al.*, 2006).

Of even greater concern, because of the seemingly inevitable effects on all calcareous marine organisms, is ocean acidification due to the increased solution of carbon dioxide that forms carbonic acid in seawater (Feely *et al.*, 2004). Measurements have already demonstrated a drop of 0.1 pH units in the oceans (Caldeira and Wickett, 2005), and laboratory and mesocosm experiments demonstrate that calcareous planktonic coccolithophores, pteropods, and foraminifera exhibit decreased calcification and growth under even mildly acidic conditions (Riebesell *et al.*, 2000; Riebesell, 2004). The biogeochemical implications are staggering. These organisms are among the greatest producers of biogenic sediments in the ocean, are vital to particle aggregation and the production of marine snow that enhances the vertical flux of biogenic material, and are major components of the cycling of carbon and the CO_2 storage capacity of the ocean (Riebesell *et al.*, 2000; Riebesell, 2004).

CORAL REEFS

Coral reefs are the most diverse marine ecosystems and among the most threatened (Knowlton, 2001; Hughes *et al.*, 2003). Just 15 years ago, many coral reef scientists still referred to coral reefs as pristine (Jackson, 1997), yet today many scientists believe that the cumulative forces of overfishing, pollution, and climate change are so great that coral reefs may virtually disappear within a few decades (Hoegh-Guldberg *et al.*, 2007; Knowlton and Jackson, 2008).

Demise of Reef Fauna

Corals are dying out around the world and are being replaced by fleshy macroalgae or algal turfs that may carpet the entire reef surface (Hughes, 1994; Pandolfi *et al.*, 2005; Newman *et al.*, 2006). In the Caribbean, live coral cover has fallen from an average of ≈55% in 1977 to 5% in 2001 (Table 1.1), whereas macroalgal cover has risen from an average of ≈5% to 40% (Gardner *et al.*, 2003; Paredes, 2007). The demise of formerly ubiquitous and abundant elkhorn and staghorn corals (*Acropora palmata* and *Acropora cervicornis*) is particularly striking; these corals were the major rock formers on shallow Caribbean reefs for at least a million years (Jackson, 1992; Aronson *et al.*, 2004; Pandolfi and Jackson, 2006) but are now officially listed as endangered species. The story is a little better in the Indo-West Pacific where live coral cover still averages ≈22%, which is about one-half of that in 1980 (Bruno and Selig, 2007). However, even the Great Barrier Reef, which is arguably the best-protected coral reef system in the world, has only 23% live coral cover. The only places I know of where live coral cover still averages ≈50% or more over large areas of reef are the uninhabited and protected atolls of the Central Pacific (Knowlton and Jackson, 2008).

Most Caribbean coral communities in 1977 still resembled the first detailed descriptions from the 1950s (Goreau, 1959), as well as reconstructions of Holocene and Pleistocene assemblages in the fossil record (Jackson, 1992; Pandolfi and Jackson, 2001, 2006; Aronson *et al.*, 2004), although reefs at Barbados had already lost their formerly dense populations of *Acropora* by the early 20th century (Lewis, 1984, 2002). In contrast, reef fishes throughout the entire region were only a small remnant of how they used to be (Jackson, 1997; Pandolfi *et al.*, 2003; McClenachan *et al.*, 2007), and populations declined by more than one-half again between 1977 and 2003 (Paredes, 2007). We can piece together a clear qualitative picture of what pristine Caribbean reef fish communities were like from archeological and historical analysis (Jackson, 1997; Jackson *et al.*, 2001; Pandolfi *et al.*, 2003). The extraordinary old photographs of fishing boats returning to Key West draped in giant sawfishes and sharks (Fig. 1.3) make these descriptions come alive, as do the trophy photographs of an afternoon's catch by a single charter boat of up to 16 gigantic goliath grouper, a now endangered species for which catch per unit effort (CPUE) declined 87% between 1956 and 1979 (L. McClenachan, personal communication).

FIGURE 1.3 A sporting day's catch of sawfish in the Florida Keys in the 1940s (courtesy of the Monroe County Public Library, Key West, Florida).

TABLE 1.2 Biomass of Fishes on Coral Reefs in Relation to Human Population Size per km of Reef or Reserve Status

Location	Human Population Size per km Reef or Protection Status	Fish Biomass, g/m^2
Kingman (CP)	0	1,020/530[a]
Jarvis (CP)	0	800
Palmyra (CP)	0.5	520/260[a]
Baker (CP)	0	390
Cozumel (C)	Protected	386
Kiritimati (CP)	21.1	310/130[a]
Cuba (C)	Protected	275
NW Hawaiian Islands (NCP)	Protected	240
Bahamas (C)	Protected	194
Tavunasica (WP)	2.6	140
Kenya (IO)	Protected	115
Vuaqava (WP)	6.6	103
Florida (C)	Unprotected	101
Totoya (WP)	18	80
Kabara (WP)	43.3	75
Main Hawaiian Islands (NCP)	Unprotected	70
Matuku (WP)	24.4	67
Moala (WP)	26.2	60
Bahamas (C)	Unprotected	57
Kenya (IO)	Unprotected	<40
Jamaica	Unprotected	39

NOTES: See Knowlton and Jackson (2008). C, Caribbean; CP, central Pacific; IO, Indian Ocean; NCP, north central Pacific; WP, western Pacific.

[a] Sample dates: 1997/2005.

We can put numbers on these impressions by comparison of modern Caribbean fish communities on unprotected reefs versus sites inside the few long-established marine protected areas (MPAs) where fishing is prohibited and the rules are strictly enforced (Table 1.2) (Newman *et al.*, 2006; Paredes, 2007). Unprotected reefs in the Pacific and Indian oceans are comparably overfished, although few if any as badly as Jamaica (Table 1.2) (McClanahan *et al.*, 2001, 2007; Dulvy *et al.*, 2002; Friedlander and DeMartini, 2002; Jackson, 2006). As for corals, the greatest fish biomass and largest fish occur on the uninhabited and protected atolls of the central and north central Pacific that may never have been severely degraded (Table 1.2) (Knowlton and Jackson, 2008). The highest fish biomass on these isolated atolls is 1,000 g/m^2, which is only double that on the best-protected Caribbean reefs. Piscivores comprise ≈50–85% of total fish biomass (McClanahan *et al.*, 2007; Knowlton and Jackson, 2008), most of it large sharks. In general, apex predators are virtually absent from reefs where fish biomass is <100 g/m^2 but may exceed the combined biomass of all lower trophic levels of fishes when fish biomass exceeds ≈300 g/m^2. Thus, when fish biomass is high, the fish trophic pyramid is upside down (Jackson, 2006; Sandin *et al.*, 2008).

Reefs in Florida surveyed in 2005 (Newman *et al.*, 2006) were also surveyed in 1880 (McClenachan *et al.*, 2007). Only 30% of the 20 species that were common in 1880 were still common in 2005, and 40% of the formerly common species were absent in 2005. Most remarkably, 4 of the 20 formerly common species in 1880 are now listed as endangered or critically endangered, including the Nassau grouper (*Epinephalus striatus*), which was the mainstay of fish sandwiches in the Florida Keys for too many decades to the point that this once fantastically abundant species is entirely fished out.

Fishes and corals are not the only animals to have declined precipitously. Harvests of Florida commercial sponges peaked in 1924 at >3 million tons, and then crashed to nearly zero in the 1940s when stricken by disease (McClenachan, 2008). Today, the sponges have recovered to ≈11% of their abundance in the 1880s. The formerly abundant sea urchin *Diadema antillarum* also declined by 90–95% because of an outbreak of an unidentified disease in 1983 (Lessios *et al.*, 1984), and much of the mortality of elkhorn and staghorn corals in the 1970s and 1980s was also due to outbreaks of disease (Aronson and Precht, 2001; Knowlton, 2001). Green turtles have declined by well over 99% from approximately 90 million in the 18th century to perhaps 300,000 today, and hawksbill turtles declined as precipitously from approximately 11 million to 30,000 (McClenachan *et al.*, 2006). The total population of the extinct Caribbean monk seal in the 18th century was ≈230,000–340,000, abundance so great that all of the remaining fish on Caribbean coral reefs would be inadequate to sustain them (McClenachan and Cooper, 2008).

Indirect Effects of Exploitation

The restriction of abundant fish biomass to protected reefs shows that MPAs do work, oceanographic factors notwithstanding, so long as they are large, well protected, and enforced (Mora *et al.*, 2006; Newman *et al.*, 2006; Knowlton and Jackson, 2008). The more difficult question concerns the potential of protection from fishing to help to restore coral populations in the face of epidemic disease and global climate change (Friedlander and DeMartini, 2002; Hughes *et al.*, 2003, 2007; Knowlton and Jackson, 2008). As for oysters in estuaries, overfishing, increased macroalgal abundance, and degraded water quality act synergistically to decrease coral growth, recruitment, and survival. Increased abundance of fleshy macroalgae and algal turfs may kill corals directly by overgrowth or indirectly by leaking of dissolved organic matter into the surrounding water that destabilizes microbial communities on corals and promotes coral disease (Nugues *et al.*, 2004; Kline *et al.*, 2006; JE Smith *et al.*, 2006; Hoegh-Guldberg *et al.*, 2007), or by smothering the crustose coralline algae that are necessary cues for coral larvae to recruit (Carpenter and Edmunds, 2006). Increased abundance of fish or sea urchins is associated with a decline in macroalgae (Newman *et al.*, 2006; Mumby *et al.*, 2007) and increased coral recruitment (Carpenter and Edmunds, 2006). Coral cover has not increased, however, presumably because of the slow growth and long generation times of corals compared with fish and macroalgae (Jackson, 1991; Pandolfi *et al.*, 2005; Newman *et al.*, 2006).

Ocean Warming and Acidification

Rising temperatures and falling pH are as ominous for the future of corals and coral reefs (Knowlton, 2001; Hughes *et al.*, 2003; Kleypas *et al.*, 2006; Hoegh-Guldberg *et al.*, 2007) as for calcareous plankton (Riebesell, 2004). Warming has caused mass mortality of corals by coral bleaching that has increased in frequency and intensity over the past two to three decades. Reduction of pH reduces coral growth rates and skeletal density, and may eventually stop calcification entirely, so that corals lose their skeletons and resemble small colonial sea anemones (Fine and Tchernov, 2007). Regardless of whether or not the corals can survive under such circumstances, reef formation would be severely reduced or halted if acidification proceeded at current rates.

Climate change exacerbates local stress due to overfishing and decline in water quality (Pandolfi *et al.*, 2005; Newton *et al.*, 2007; Knowlton and Jackson, 2008), but the reverse is also true to the extent that the unpopulated, unfished, and unpolluted atolls of the central Pacific still possess ≈50% coral cover while other reefs in the Pacific have less than half that amount (Bruno and Selig, 2007; McClanahan *et al.*, 2007; Knowlton and Jackson, 2008). This is the only good news I know of for coral reefs, and there is a pressing need to study these reefs to determine why corals have so far persisted in such abundance and the degree to which coral community composition is shifting toward more physiologically resilient species or to those with shorter generation times and faster growth. Ultimately, however, it is difficult to imagine how corals will be able to survive or reefs persist if the rise in CO_2 continues unabated.

THE FUTURE OCEAN

The overall status of the four major categories of ocean ecosystems and the principal drivers of their degradation are summarized in Table 1.3.

TABLE 1.3 Status and Trends of Major Ocean Ecosystems Defined by Principal Symptoms and Drivers of Degradation in the >99% of the Global Ocean That Is Unprotected from Exploitation

Coral reefs: Critically endangered

Symptoms: Live coral reduced 50–93%; fish populations reduced 90%; apex predators virtually absent; other megafauna reduced by 90–100%; population explosions of seaweeds; loss of complex habitat; mass mortality of corals from disease and coral bleaching

Drivers: Overfishing, warming and acidification due to increasing CO_2, runoff of nutrients and toxins, invasive species

Estuaries and coastal seas: Critically endangered

Symptoms: Marshlands, mangroves, seagrasses, and oyster reefs reduced 67–91%; fish and other shellfish populations reduced 50–80%; eutrophication and hypoxia, sometimes of entire estuaries, with mass mortality of fishes and invertebrates; loss of native species; toxic algal blooms; outbreaks of disease; contamination and infection of fish and shellfish; human disease

Drivers: Overfishing; runoff of nutrients and toxins; warming due to rise of CO_2; invasive species; coastal land use

Continental shelves: Endangered

Symptoms: Loss of complex benthic habitat; fishes and sharks reduced 50–99%; eutrophication and hypoxia in "dead zones" near river mouths; toxic algal blooms; contamination and infection of fish and shellfish; decreased upwelling of nutrients; changes in plankton communities

Drivers: Overfishing; trophic cascades; trawling; runoff of nutrients and toxins; warming and acidification due to rise of CO_2; introduced species; escape of aquaculture species

Open ocean pelagic: Threatened

Symptoms: Targeted fishes reduced 50–90%; increase in nontargeted fish; increased stratification; changes in plankton communities

Drivers: Overfishing; trophic cascades; warming and acidification due to rise of CO_2

Coastal ecosystems are endangered to critically endangered on a global scale. The lesser endangerment of pelagic ecosystems reflects their remoteness from all factors except fishing and climate change, although there are no real baselines for comparison to critically evaluate changes in plankton communities. This grim assessment begs the question, What are the projected long-term consequences for the ecological condition of the ocean if we continue with business as usual?

Predicting the future is, at best, a highly uncertain enterprise. Nevertheless, I believe we have a sufficient basic understanding of the ecological processes involved to make meaningful qualitative predictions about what will happen in the oceans if humans fail to restrain their style of exploitation and consumption. Failure to stop overfishing will push increasing numbers of species to the brink of extinction—perhaps irreversibly as for Newfoundland cod—except for small, opportunistic species. Unrestrained runoff of nutrients and toxins, coupled with rising temperatures, will increase the size and abundance of dead zones and toxic blooms that may merge all along the continents. Even farmed seafood will be increasingly toxic and unfit for human consumption unless grown in isolation from the ocean. Outbreaks of disease will increase. Failure to cap and reduce emissions of CO_2 and other greenhouse gases will increase ocean temperatures and intensify acidification. Warmer and lighter surface waters will inhibit vertical mixing of the ocean, eventually leading to hypoxia or anoxia below the thermocline as in the Black Sea. Biogeochemical cycles will be perturbed in uncertain ways as they have been in the past (Knoll, 2003). Mass extinction of multicellular life will result in profound loss of animal and plant biodiversity, and microbes will reign supreme.

These predictions will undoubtedly appear extreme, but it is difficult to imagine how such changes will not come to pass without fundamental changes in human behavior. Moreover, as we have seen, all of these trends have actually been measured to a limited degree in the past few decades. The oceans are becoming warmer and more acidic; eutrophication, hypoxia, and the numbers and sizes of dead zones are increasing in quantity and size; vertical mixing of the open ocean is measurably decreasing; and many of our most valuable fisheries have collapsed and failed to recover. Some may say that it is irresponsible to make such predictions pending further detailed study to be sure of every point. However, we will never be certain about every detail, and it would be irresponsible to remain silent in the face of what we already know.

HOW CAN WE STOP THE DEGRADATION OF THE OCEANS?

The three major drivers of ecosystem degradation are overexploitation, nutrient and toxic pollution, and climate change. The challenges of bringing these threats under control are enormously complex and will require fundamental changes in fisheries, agricultural practices, and the ways we obtain energy for everything we do. We have to begin somewhere, however, and the following very significant actions could begin right away without further scientific research or technological innovation.

Sustainable Fisheries

The tools for effective management of wild fisheries are well established (Beddington *et al.*, 2007; Hilborn, 2007), and there are encouraging examples of success (Safina *et al.*, 2005). Nevertheless, the required actions have rarely been implemented (Rosenberg *et al.*, 2006). In contrast, subsistence overfishing in developing nations is commonly a matter of survival, so that alternative sources of protein and livelihood are required to bring the situation under control (McClanahan *et al.*, 2006; Hilborn, 2007). More fundamentally, however, wild fisheries cannot possibly sustain increasing global demand regardless of how well they are managed. Industrial scale aquaculture of species low on the food chain is the only viable alternative. But this in turn will require strong new regulation to prevent harmful ecosystem consequences such as the destruction of mangroves for shrimp farms and the impacts on wild salmon populations caused by the explosion of parasitic copepods that infect salmon farms in British Columbia (Goldberg and Naylor, 2005; Krkosek *et al.*, 2007). Despite all of these concerns, however, the only thing standing in the way of sustainable fisheries and aquaculture is the lack of political will and the greed of special interests. Simply enforcing the standards of the Magnuson–Stevens Act and the U.S. National Marine Fisheries Service would result in major improvements in United States waters within a decade (Safina *et al.*, 2005; Rosenberg *et al.*, 2006).

Coastal Pollution and Eutrophication

Heavily subsidized overuse of chemical fertilizers and pesticides, poor soil management practices, and unregulated animal production systems are the major sources of excess nitrogen and other nutrients in the environment that fuel coastal eutrophication (Jackson *et al.*, 2001; Rabalais *et al.*, 2007; Turner *et al.*, 2008) and severely degrade terrestrial ecosystems (Tilman *et al.*, 2002; Clay, 2004; Galloway *et al.*, 2004; Dale and Polasky, 2007). Manufacture of chemical fertilizers also consumes huge amounts of energy from natural gas (Howarth, 2004). Removal of subsidies and taxation of fertilizers would significantly reduce nutrient loading, eutrophication, and emissions of greenhouse gases with only modest decreases in food production and increased costs.

Climate Change and Ocean Acidification

The rise in greenhouse gases and the resulting global economic, social, and environmental consequences comprise the greatest challenge to humanity today. Moderation of consumption of fossil fuels in a time of rising global aspirations and finding alternative sources of energy will require all of the ingenuity humanity can muster and will preoccupy us for the remainder of the century. The problems appear so overwhelming that many are ready to write off coral reefs and all of the other marine life that will be drastically affected. But such defeatism belies the growing realization that local protection from overexploitation and pollution confers some as yet poorly understood level of resistance and resilience to the effects of climate change on coral reefs (Dulvy *et al.*, 2002; Hughes *et al.*, 2007; Knowlton and Jackson, 2008), and the same is very likely true for other marine ecosystems. This is an important area for new scientific research to better understand the synergies among different drivers of ecosystem change and their likely consequences. Most importantly, local conservation measures may help to buy time for marine ecosystems until we bring the rise of greenhouse gases under more effective control.

ACKNOWLEDGMENTS

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2

Are We in the Midst of the Sixth Mass Extinction? A View from the World of Amphibians

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Many scientists argue that we are either entering or in the midst of the sixth great mass extinction. Intense human pressure, both direct and indirect, is having profound effects on natural environments. The amphibians—frogs, salamanders, and caecilians—may be the only major group currently at risk globally. A detailed worldwide assessment and subsequent updates show that one-third or more of the 6,300 species are threatened with extinction. This trend is likely to accelerate because most amphibians occur in the tropics and have small geographic ranges that make them susceptible to extinction. The increasing pressure from habitat destruction and climate change is likely to have major impacts on narrowly adapted and distributed species. We show that salamanders on tropical mountains are particularly at risk. A new and significant threat to amphibians is a virulent, emerging infectious disease, chytridiomycosis, which appears to be globally distributed, and its effects may be exacerbated by global warming. This disease, which is caused by a fungal pathogen and implicated in serious declines and extinctions of >200 species of amphibians, poses the greatest threat to biodiversity of any known disease. Our data for frogs in the Sierra Nevada of California show that the

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fungus is having a devastating impact on native species, already weakened by the effects of pollution and introduced predators. A general message from amphibians is that we may have little time to stave off a potential mass extinction.

Biodiversity is a term that refers to life on Earth in all aspects of its diversity, interactions among living organisms, and, importantly, the fates of these organisms. Scientists from many fields have raised warnings of burgeoning threats to species and habitats. Evidence of such threats (e.g., human population growth, habitat conversion, global warming and its consequences, impacts of exotic species, new pathogens, etc.) suggests that a wave of extinction is either upon us or is poised to have a profound impact.

The title of this chapter is an appropriate question at this stage of the development of biodiversity science. We examine the topic at two levels. We begin with a general overview of past mass extinctions to determine where we now stand in a relative sense. Our specific focus, however, is a taxon, the Class Amphibia. Amphibians have been studied intensively since biologists first became aware that we are witnessing a period of their severe global decline. Ironically, awareness of this phenomenon occurred at the same time the word "biodiversity" came into general use, in 1989.

FIVE MASS EXTINCTIONS

It is generally thought that there have been five great mass extinctions during the history of life on this planet (Jablonski, 1995; Erwin, 2001). [The first two may not qualify because new analyses show that the magnitude of the extinctions in these events was not significantly higher than in several other events (Alroy, Chapter 11, this volume).] In each of the five events, there was a profound loss of biodiversity during a relatively short period.

The oldest mass extinction occurred at the Ordovician–Silurian boundary (≈439 Mya). Approximately 25% of the families and nearly 60% of the genera of marine organisms were lost (Jablonski, 1995; Erwin, 2001). Contributing factors were great fluctuations in sea level, which resulted from extensive glaciations, followed by a period of great global warming. Terrestrial vertebrates had not yet evolved.

The next great extinction was in the Late Devonian (≈364 Mya), when 22% of marine families and 57% of marine genera, including nearly all jawless fishes, disappeared (Jablonski, 1995; Erwin, 2001). Global cooling after bolide impacts may have been responsible because warm water taxa were most strongly affected. Amphibians, the first terrestrial vertebrates, evolved in the Late Devonian, and they survived this extinction event (Clack, 2002).

The Permian–Triassic extinction (≈251 Mya) was by far the worst of the five mass extinctions; 95% of all species (marine as well as terrestrial) were lost, including 53% of marine families, 84% of marine genera, and 70% of land plants, insects, and vertebrates (Jablonski, 1995; Erwin, 2001). Causes are debated, but the leading candidate is flood volcanism emanating from the Siberian Traps, which led to profound climate change. Volcanism may have been initiated by a bolide impact, which led to loss of oxygen in the sea. The atmosphere at that time was severely hypoxic, which likely acted synergistically with other factors (Huey and Ward, 2005). Most terrestrial vertebrates perished, but among the few that survived were early representatives of the three orders of amphibians that survive to this day (Marjanovic and Laurin, 2007; Cannatella *et al.*, in press).

The End Triassic extinction (≈199–214 Mya) was associated with the opening of the Atlantic Ocean by sea floor spreading related to massive lava floods that caused significant global warming. Marine organisms were most strongly affected (22% of marine families and 53% of marine genera were lost) (Jablonski, 1995; Erwin, 2001), but terrestrial organisms also experienced much extinction. Again, representatives of the three living orders of amphibians survived.

The most recent mass extinction was at the Cretaceous–Tertiary boundary (≈65 Mya); 16% of families, 47% of genera of marine organisms, and 18% of vertebrate families were lost. Most notable was the disappearance of nonavian dinosaurs. Causes continue to be debated. Leading candidates include diverse climatic changes (e.g., temperature increases in deep seas) resulting from volcanic floods in India (Deccan Traps) and consequences of a giant asteroid impact in the Gulf of Mexico (Jablonski, 1995; Erwin, 2001). Not only did all three orders of amphibians again escape extinction, but many, if not all, families and even a number of extant amphibian genera survived (Vieites *et al.*, 2007).

A SIXTH EXTINCTION?

The possibility that a sixth mass extinction spasm is upon us has received much attention (Novacek, 2007). Substantial evidence suggests that an extinction event is underway.

When did the current extinction event begin? A period of climatic oscillations that began about 1 Mya, during the Pleistocene, was characterized by glaciations alternating with episodes of glacial melting (Barnosky, Chapter 12, this volume). The oscillations led to warming and cooling that impacted many taxa. The current episode of global warming can be considered an extreme and extended interglacial period; however, most geologists treat this period as a separate epoch, the Holocene, which began ≈11,000 years ago at the end of the last glaciation. The Holocene extinctions were greater than occurred in the Pleistocene, especially with respect to large terrestrial vertebrates. As in previous extinction events, climate is thought to have played an important role, but humans may have had compounding effects. The overkill hypothesis (Martin, 2005) envisions these extinctions as being directly human-related. Many extinctions occurred at the end of the Pleistocene, when human impacts were first manifest in North America, in particular, and during the early Holocene. Because naive prey were largely eliminated, extinction rates decreased. Extinctions were less profound in Africa, where humans and large mammals coevolved. Most currently threatened mammals are suffering from the effects of range reduction and the introduction of exotic species (MacPhee and Marx, 1997). In contrast to the overkill hypothesis, an alternative explanation for the early mammalian extinctions is that human-mediated infectious diseases were responsible (MacPhee and Flemming, 1999).

Many scientists think that we are just now entering a profound spasm of extinction and that one of its main causes is global climate change (Thomas *et al.*, 2004; Parry *et al.*, 2007; Jackson, Chapter 1, this volume). Furthermore, both global climate change and many other factors (e.g., habitat destruction and modification) responsible for extinction events are directly related to activities of humans. In late 2007, there were 41,415 species on the International Union for Conservation of Nature Red List (International Union for the Conservation of Nature, 2007), of which 16,306 are threatened with extinction; 785 are already extinct. Among the groups most affected by the current extinction crisis are the amphibians.

AMPHIBIANS IN CRISIS

Amphibians have received much attention during the last two decades because of a now-general understanding that a larger proportion of amphibian species are at risk of extinction than those of any other taxon (SN Stuart *et al.*, 2004). Why this should be has perplexed amphibian specialists. A large number of factors have been implicated, including most prominently habitat destruction and epidemics of infectious disease (Pechmann and Wake, 2006); global warming also has been invoked as a contributing factor (Pounds *et al.*, 2006). What makes the amphibian case so compelling is the fact that amphibians are long-term survivors that have persisted through the last four mass extinctions.

Paradoxically, although amphibians have proven themselves to be survivors in the past, there are reasons for thinking that they might be vulnerable to current environmental challenges and, hence, serve as multipurpose sentinels of environmental health. The typical life cycle of a frog involves aquatic development of eggs and larvae and terrestrial activity as adults, thus exposing them to a wide range of environments. Frog larvae are typically herbivores, whereas adults are carnivores, thus exposing them to a wide diversity of food, predators, and parasites. Amphibians have moist skin, and cutaneous respiration is more important than respiration by lungs. The moist, well-vascularized skin places them in intimate contact with their environment. One might expect them to be vulnerable to changes in water or air quality resulting from diverse pollutants. Amphibians are thermal-conformers, thus making them sensitive to environmental temperature changes, which may be especially important for tropical montane (e.g., cloud forest) species that have experienced little temperature variation. Such species may have little acclimation ability in rapidly changing thermal regimes. In general, amphibians have small geographic ranges, but this is accentuated in most terrestrial species (the majority of salamanders; a large proportion of frog species also fit this category) that develop directly from terrestrial eggs that have no free-living larval stage. These small ranges make them especially vulnerable to habitat changes that might result from either direct or indirect human activities.

Living amphibians (Class Amphibia, Subclass Lissamphibia) include frogs (Order Anura, ≈5,600 currently recognized species), salamanders (Order Caudata, ≈570 species), and caecilians (Order Gymnophiona, ≈175 species) (AmphibiaWeb, 2007). Most information concerning declines and extinctions has come from studies of frogs, which are the most numerous and by far the most widely distributed of living amphibians. Salamanders facing extinctions are centered in Middle America. Caecilians are the least well known; little information on their status with respect to extinction threats exists (SN Stuart *et al.*, 2004).

Amphibians are not distributed evenly around the world. Frogs and caecilians thrive in tropical regions (Fig. 2.1). Whereas caecilians do not occur outside the tropical zone, frogs extend northward even into the Arctic zone and southward to the southern tips of Africa and South America. Salamanders are mainly residents of the North Temperate zone, but one subclade (Bolitoglossini) of the largest family (Plethodontidae) of salamanders has radiated adaptively in the American tropics. The bolitoglossine salamanders comprise nearly 40% of living species of salamanders; ≈80% of bolitoglossines occur in Middle America, with only a few species ranging south of the equator.

The New World tropics have far more amphibians than anywhere else. Fig. 2.1 shows the number of species in relation to the size of countries [all data from AmphibiaWeb (2007)]. The Global Amphibian Assessment completed its first round of evaluating the status of all then-recognized species in 2004 (SN Stuart *et al.*, 2004), finding 32.5% of the known species of amphibians to be “globally threatened” by using the established top three

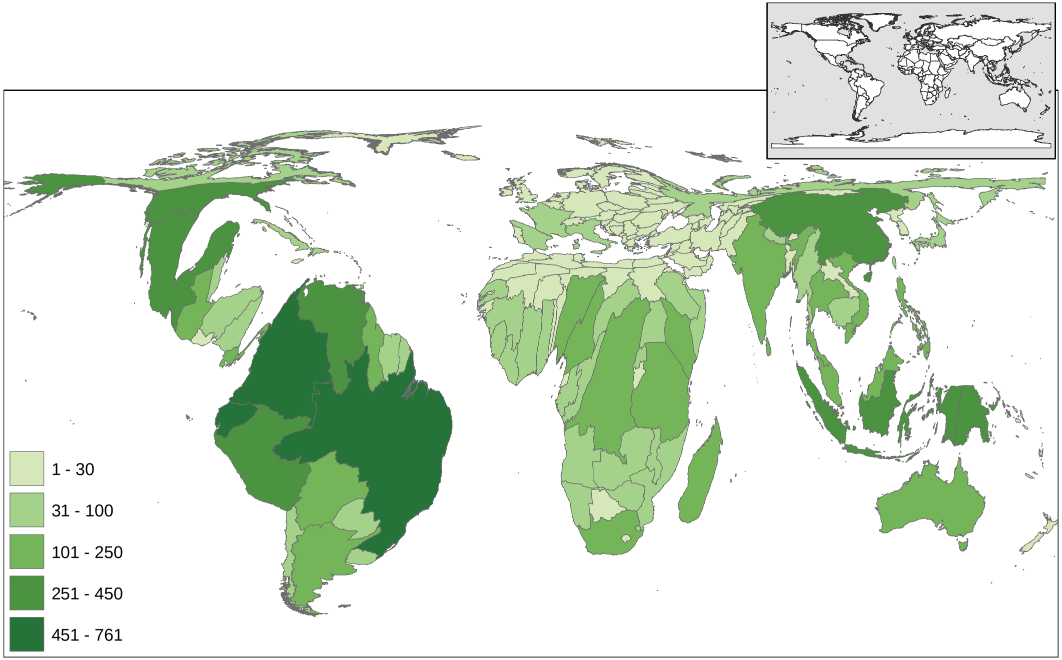

FIGURE 2.1 Global amphibian species diversity by country visualized using density-equalizing cartograms. Country size is distorted in proportion to the total number of amphibian species occurring in each country relative to its size. (*Inset*) Baseline world map. Brazil (789 species) and Colombia (642) have the largest number of species. China (335) has the largest number of species in the Old World. The Democratic Republic of the Congo (215) has the largest number from continental Africa. However, 239 species are recorded from Madagascar. Australia has 225 species, and Papua New Guinea has 289. In North America, Mexico has the largest number of species (357). There are 291 species in the United States. Prepared by M. Koo (see *Acknowledgments*).

categories of threat of extinction (i.e., Vulnerable, Endangered, or Critically Endangered); 43% of species have declining populations (International Union for the Conservation of Nature, 2007). In general, greater numbers as well as proportions of species are at risk in tropical countries (e.g., Sri Lanka with 107 species, most at risk; nontropical New Zealand has an equivalent proportion, but has only 7 species) (Fig. 2.2). Updates from the Global Amphibian Assessment are ongoing and show that, although new species described since 2004 are mostly too poorly known to be assessed, >20% of analyzed species are in the top three categories of threat (Global Amphibian Assessment, 2007). Species from montane tropical regions, especially those associated with stream or streamside habitats, are most likely to be severely threatened.

We present a case study from our own work to explore the reasons underlying declines and extinctions of amphibians.

RANA IN THE SIERRA NEVADA OF CALIFORNIA

One of the most intensively studied examples of amphibian declines comes from the Sierra Nevada of California. The mountain range spans thousands of square kilometers of roadless habitat, most of which is designated as National Park and Forest Service Wilderness Areas, the most highly protected status allowable under U.S. law. The range contains thousands of high-elevation (1,500- to 4,200-m) alpine lakes, as well as streams and meadows, that until recently harbored large amphibian populations. Biological surveys conducted nearly a century ago by Grinnell and Storer (1924) reported that amphibians were the most abundant vertebrates in the high Sierra Nevada. Because large numbers of specimens were collected from well-documented localities by these early workers, the surveys provide a foundation on which current distributions can be compared. Of the seven amphibian species that occur >1,500 m in the Sierra Nevada, five (*Hydromantes playcephalus*, *Bufo boreas*, *B. canorus*, *Rana muscosa*, and *R. sierrae*) are threatened. The best studied are the species in the family Ranidae and include the Sierra Nevada yellow-legged frog (*R. sierrae*) and southern yellow-legged frog (*R. muscosa*) (Vredenburg *et al.*, 2007). In the 1980s, field biologists became aware that populations were disappearing (Bradford, 1989), but the extent of the problem was not fully appreciated until an extensive resurvey of the Grinnell-Storer (1924) sites disclosed dramatic losses (Drost and Fellers, 1996). Especially alarming was the discovery that frogs had disappeared from 32% of the historical sites in Yosemite National Park. Furthermore, populations in most remaining sites had been reduced to a few individuals.

The yellow-legged frogs, which had been nearly ubiquitous in high-elevation sites in the early 1980s, are ideal subjects for ecological study.

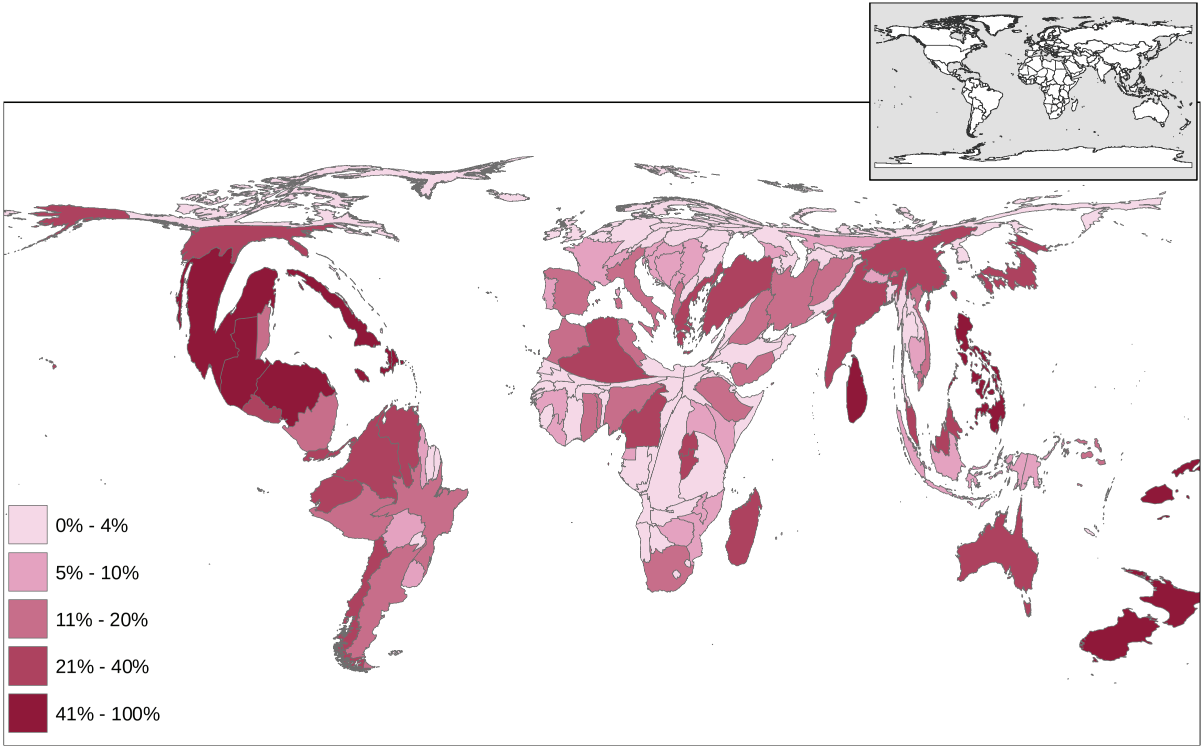

FIGURE 2.2 Percentage of amphibian fauna in each country in the top three categories of threat (Critically Endangered, Endangered, and Threatened) (Global Amphibian Assessment, 2007). (*Inset*) Baseline world map. Visualization based on density-equalizing cartograms prepared by M. Koo.

Their diurnal habits and their use of relatively simple and exposed alpine habitats make them readily visible and easy to capture. Typically these frogs occurred in large populations, and rarely were they found >2 m from the shores of ponds, lakes, and streams. Censuses throughout the Sierra Nevada began in the early 1990s and intensified in this century. Although most of the frog habitat in this large mountain range is protected in national parks and wilderness areas, yellow-legged frogs are now documented to have disappeared from >90% of their historic range during the last several decades (Vredenburg *et al.*, 2007). The most recent assessment lists them as Critically Endangered (SN Stuart *et al.*, 2004). Factors implicated in the declines include introduced predatory trout (Knapp and Matthews, 2000), disease (Rachowicz *et al.*, 2006), and air pollution (Davidson *et al.*, 2001; Davidson, 2004). Experiments that extirpated introduced trout led to rapid recovery of frog populations (Vredenburg, 2004). Thus, for a time, there was hope that, simply by removing introduced trout, frog populations would persist and eventually spread back into formerly occupied habitat. Curiously, multiple attempts at reintroduction in the more western parts of the range clearly failed (Fellers *et al.*, 2007). Hundreds of dead frogs were encountered at both reintroduction and many other sites in the western part of the range (Rachowicz *et al.*, 2006), and it became apparent that predation was not the only factor affecting the frogs' survival.

In 2001, chytridiomycosis, a disease of amphibians caused by a newly discovered pathogenic fungus [*Batrachochytrium dendrobatidis* (Bd)] (Berger *et al.*, 1998) was detected in the Sierra Nevada (Fellers *et al.*, 2001). Subsequently, a retrospective study disclosed that Bd was found on eight frogs (*R. muscosa*, wrongly identified as *R. boylii*) collected on the west edge of Sequoia and Kings Canyon national parks in 1975 (Oullet *et al.*, 2005). Infected tadpoles of these species are not killed by Bd. When tadpoles metamorphose, the juveniles became reinfected and usually die (Rachowicz and Vredenburg, 2004). However, tadpoles of yellow-legged frogs in the high Sierra Nevada live for 2 to 4 years, so even if adults and juveniles die, there is a chance that some individuals might survive if they can avoid reinfection after metamorphosis.

The disease is peculiar in many ways (Daszak *et al.*, 2003; Mitchell *et al.*, 2008). Pathogenicity is unusual for chytrid fungi, and Bd is the first chytrid known to infect vertebrates. The pathogen, found only on amphibians, apparently lives on keratin, present in tadpoles on the external mouth parts and in adults in the outer layer of the skin. The life cycle includes a sporangium in the skin, which sheds flagellated zoospores outside of the host. The zoospores then infect a new host or reinfect the original host, establishing new sporangia and completing the asexual life cycle. Sexual reproduction, seen in other chytrids, is unknown in Bd (Morgan *et al.*, 2007). Much remains to be learned about the organism (Mitchell *et al.*, 2008). For example, despite its aquatic life cycle, Bd has been found on fully terrestrial species of amphibians that never enter water, and the role of zoospores in these forms is uncertain. No resting stage has been found, and no alternative hosts are known. Vectors have not been identified. It is relatively easy to rid a healthy frog of the fungus by using standard fungicides (Parker *et al.*, 2002). Yet the fungus is surprisingly virulent. Finally, and importantly, how the fungus causes death is not clear, although it is thought to interfere with oxygen exchange and osmoregulation (Voyles *et al.*, 2007).

With associates, we have been studying frog populations in alpine watersheds within Yosemite, Sequoia, and Kings Canyon national parks for over a decade. We recently showed that yellow-legged frogs are genetically diverse (Vredenburg *et al.*, 2007). Mitochondrial DNA sequence data identified six geographically distinct haplotype clades in the two species of frogs, and we recommended that these clades be used to define conservation goals. Population extinctions, based on historical records, ranged from 91.3% to 98.1% in each of the six clades, so challenges for conservation are daunting. In the last 5 years, we have documented mass die-offs (Fig. 2.3) and the collapse of populations due to chytridiomycosis outbreaks (Rachowicz *et al.*, 2006). Although the mechanism of spread is unknown, it may involve movements of adult frogs among lakes within basins or possibly movements of a common, more vagile, and terrestrial frog, *Pseudacris regilla* (on which Bd has been detected), ahead of the *Rana* infection wave. Mammals, birds, or insects also are possible vectors. We have followed movements of *R. muscosa* and *R. sierrae* using pit tags and

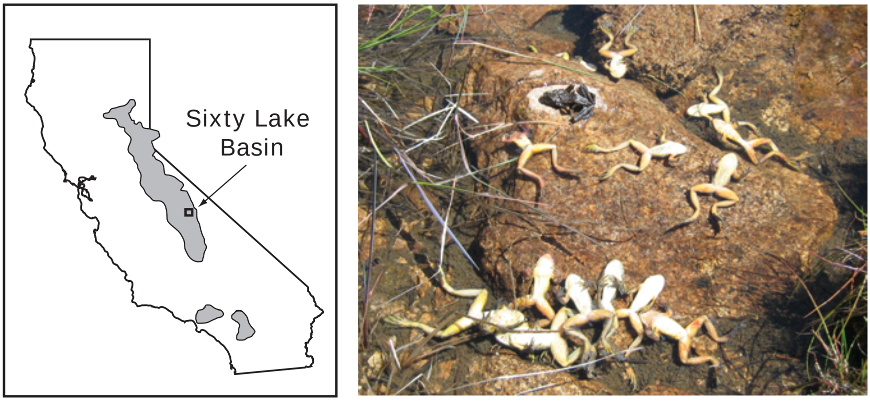

FIGURE 2.3 Distribution of the critically endangered yellow-legged frogs in California. Chytridiomycosis outbreaks have had devastating effects (*Rana muscosa* photographed in Sixty Lake Basin, August 15, 2006).

radio tracking from 1998 to 2002 (Vredenburg *et al.*, 2004), and we believe that movement between local populations may be spreading the disease. The environment in this area (2,500–3,300 m) is harsh for amphibians, with isolated ponds separated by inhospitable solid granite that lacks vegetation. Small streams join many of the lakes in each basin. The maximum movement of frogs, (≈400 m) was in and near streams; most movements are <300 m. Our results are compatible with those of another study (Pope and Matthews, 2001), which included a report of a single overland movement event. If chytridiomycosis sweeps through the Sierra Nevada the way it has through Central America (Lips *et al.*, 2006), then population and metapopulation extinctions may be a continuing trend; we may be on the verge of losing both species.

It might be possible to arrest an epidemic. Laboratory treatments have shown that infected animals can be cleared of infection within days (Parker *et al.*, 2002); if the dynamics of the disease can be altered or if animals can survive long enough to mount an immunological defense, then survival might be possible. Survival of infected frogs after an apparent outbreak has been seen in Australia (Retallick *et al.*, 2004), but is unknown in the Sierra Nevada frogs. The yellow-legged frogs of the Sierra Nevada are an ideal species in which to test this because they live in discreet habitat patches, are relatively easy to capture, and are highly philopatric.

COMMON THEMES IN AMPHIBIAN DECLINES

In the early 1990s, there was considerable debate about whether amphibians were in general decline or only local fluctuations in population densities were involved (Blaustein, 1994; Pechmann and Wilbur, 1994). A definitive 5-year study that involved daily monitoring of a large amphibian fauna at the Monteverde Cloud Forest Preserve in Costa Rica showed that 40% (20 species of frogs) of the species had been lost (Pounds *et al.*, 1997). These instances involved some extraordinary species, such as the spectacularly colored golden toad (*Bufo periglenes*) and the harlequin frog (*Atelopus varius*). Particularly striking about this case is the highly protected status of the preserve, so habitat destruction, the most common reason for species disappearances in general, can be excluded. The start of this decline was pinpointed to the late 1980s. At about the same time, disappearances of species from protected areas in the Australian wet tropics were recorded (McDonald, 1990). Both species of the unique gastric brooding frogs from Australia (*Rheobatrachus*) disappeared. Declines in other parts of the world included most species of the generally montane, diurnal frogs of the genus *Atelopus* from South and lower Central America, and species of *Bufo* and *Rana* from the Sierra Nevada of California (Bradford, 1989; Retallick *et al.*, 2004; Pounds *et al.*, 2006). At first all of these declines were enigmatic, but eventually two primary causal factors emerged: the infectious disease chytridiomycosis and global warming (Lips *et al.*, 2006; Pounds *et al.*, 2006).

Chytridiomycosis was detected almost simultaneously in Costa Rica and Australia (Berger *et al.*, 1998). From the beginning, it was perceived as a disease with devastating consequences. It quickly swept through Costa Rica and Panama, leaving massive declines and local extinctions in its wake (Lips *et al.*, 2006). More than half of the amphibian species in lower montane forest habitats suffered declines on the order of 80%, and several disappeared. This extinction event had been predicted on the assumption that chytridiomycosis would continue its sweep southward from Monteverde, in northwestern Costa Rica, to El Cope in central Panama (Lips *et al.*, 2006). Attention is now focused on eastern Panama and northwestern Colombia, where chythridiomycosis has not yet had evident impact.

Carcasses of animals from the Monteverde extinction event are not available, and it is not known whether Bd was responsible for frog deaths. However, Bd has been detected in many preserved specimens that were collected at different elevations along an altitudinal transect in Braulio Carrillo National Park in 1986 (Puschendorf *et al.*, 2006). The park is in northern Costa Rica ≈100 km southeast of Monteverde. Given the high prevalence of Bd in the specimens surveyed, it seems reasonable to assume that Bd also was present at Monteverde. Of course, there are many more species present in tropical areas (67 at El Cope, Panama) (Lips *et al.*, 2006) than in the Sierra Nevada (7 at high elevations, but 3 most commonly, only 2 of which are aquatic), and hence there are many more opportunities for the spread of Bd among tropical species. The average moisture content of the air in the tropical environments is doubtless much higher, on average, in Central America than in the Sierra Nevada, where a characteristic dry summer rainfall pattern prevails and where there is no forest canopy because of the altitude and substrate. Although we do not know the mechanism of spread, conditions in Central America appear more suitable for the spread of an aquatic fungus.

Amphibians tend to have broader ranges in temperate regions than in the tropics. Despite many population extinctions in temperate regions, there have been few extinctions. Accordingly, the tropical species of amphibians are more at risk, but not just because of their typically small geographic ranges. Because they occur in rich, multispecies communities, the species become infected simultaneously.

Climate change has been implicated in declines since the documentation of disappearances at Monteverde (Pounds *et al.*, 1999; Still *et al.*, 1999). Unusual weather conditions were initially implicated with amphibian declines. Large increases in average tropical air and sea surface temperatures were associated with El Niño events in the late 1980s; substantial warming had already occurred since the early 1970s. Temperature increases were correlated with increases in the height at which clouds formed at Monteverde and consequent reductions in the deposition of mist and cloud water critical for maintenance of cloud forest conditions during the dry season (Pounds *et al.*, 2006). Simulations using global climate models showed that greenhouse warming could have the effect of raising the cloud line by as much as 500 m at Monteverde during the dry season (Still *et al.*, 1999; Pounds *et al.*, 2006).

A more general effect of climate change has been proposed for the disappearance of 100 species of tropical montane frogs of the genus *Atelopus*, which is widespread in southern Central and northern South America. A detailed correlational analysis revealed that ≈80 species were last seen immediately after a warm year (Pounds *et al.*, 2006). Several species disappeared from Ecuador during 1987–1988, which included the most extreme combination of dry and warm conditions in 90 years (Ron *et al.*, 2003). Authors of that article document that the mean annual temperature in the Ecuadorian Andes has increased by ≈2°C during the last century.

Pounds and coworkers (2006) hypothesized that climate change, precipitation, and increased temperature have acted synergistically in favor of the growth of the infectious chytrid fungus. They argue that global warming has shifted temperatures closer to the presumed optimal conditions for *B. dendrobatidis* at Monteverde and the other intermediate elevation areas of the Central and South American highlands, where most of the extinctions of *Atelopus* have occurred. Warming has increased cloud cover in these areas, which had the effect of elevating already higher nighttime temperatures, thus favoring fungal growth. The hypothesis has yet to be tested.

IS GLOBAL WARMING A REAL EXTINCTION THREAT?

The Intergovernmental Panel on Climate Change (IPCC) reached consensus that climate change is happening and that it is largely related to human activities (Parry *et al.*, 2007). Estimates of global warming during the next century vary, but generally fall in the range of 2°C to 4°C, whereas rises as high as 7°C are projected for much of the United States and Europe, with even higher temperatures expected in northern Eurasia, Canada, and Alaska (Parry *et al.*, 2007). Such rises would have devastating effects on narrowly distributed montane species, such as cloud forest and mountaintop salamanders and frogs in Middle and South America. The physiology of ectotherms such as amphibians and their ability to acclimate also are important considerations for these species (Calosi *et al.*, 2008). With climate change (already 2°C changes in temperature have been recorded in montane Ecuador) (Ron *et al.*, 2003), altitudinal limits of plant and animal communities will shift upward and amphibians must either move with them or acclimate until adaptation occurs. Even small increases in temperature lead to significant metabolic depression in montane salamanders (Bernardo and Spotila, 2006). Impacts of the different warming scenarios are all dramatic and severe [see fig. TS.6 in Parry *et al.* (2007)]. The first event predicted by the IPCC panel, "Amphibian Extinctions Increasing on Mountains," is now an empirical fact.

In previous publications, we showed that many tropical plethodontid salamanders have very narrow altitudinal limits and are often restricted to single mountains or local mountain ranges (Wake *et al.*, 1991). With few exceptions, species found above 1,500–2,000 m have narrow distributional limits. We have surveyed extensively a mountainous segment of eastern Mexico from the vicinity of Cerro Cofre de Perote (≈4,000 m) in central western Veracruz in the north to Cerro Pelon (≈3,000 m) in northern Oaxaca in the south. These two peaks, separated by ≈280 km, lie along the eastern crest of the Sierra Madre Oriental, a nearly continuous range that is broken only by Rio Santo Domingo (Fig. 2.4). Otherwise the crest lies above 1,500 m, with many peaks that rise to ≈2,000 m or higher. There are 18 species of plethodontids on both Cofre de Perote and Pelon, but only two species—widespread lowland members of *Bolitoglossa*—are shared. To determine the geographical limits of the other species, we have been surveying the entire crest area since the 1970s. We have learned that most of the species on each mountain are endemic to it. When we searched in the intervening region, expecting to expand the known distributional ranges for different species, we instead discovered numerous undescribed species (many since named) almost every time we explored an isolated peak at >2,000 m. On a single short trip just 5 years ago to the Sierra de Mazateca, north of the Rio Santo Domingo (Fig. 2.4), we discovered two new species of *Pseudoeurycea* and at least one new species of *Thorius* (Parra-Olea *et al.*, 2005). We suspect that many species disappeared without ever having been discovered because the area is heavily populated and has experienced extensive habitat modification. Furthermore, the newly discovered species are endangered and survive in what appear to be suboptimal, disturbed habitats or in small fragments of forest. The majority of species along altitudinal transects in this area are found at >2,000 m in cloud forests that are being forced upward by global warming. On Cerro Pelon, eight of the species are found only at >2,200 m, and six of them range to the top of the mountain. Global warming threatens to force them off the mountain and into extinction.

The section of the Sierra Madre Oriental we have been studying is home to 17 named and 3–5 as yet unnamed species of the plethodontid salamander genus *Thorius*, the minute salamanders. All but four of these species occur exclusively at >2,000 m, often on mountains that rise only

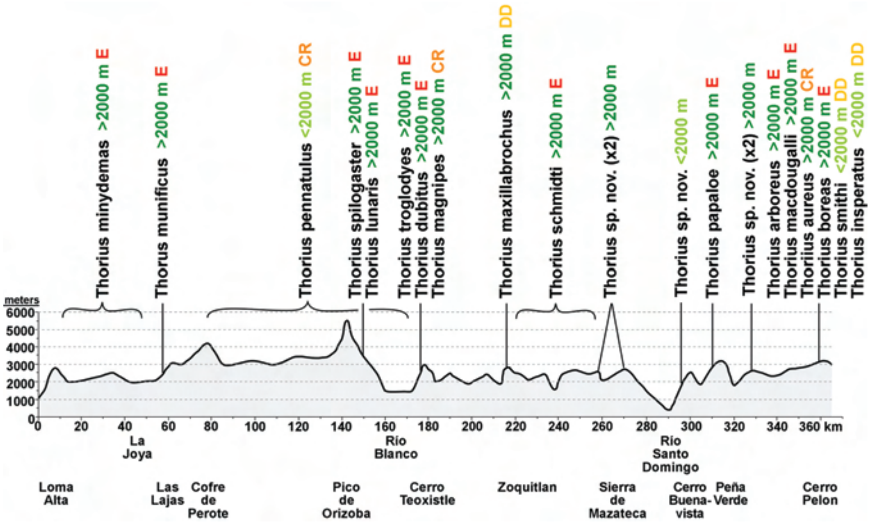

FIGURE 2.4 A diagrammatic profile of the Sierra Madre Oriental from north-central Veracruz to northern Oaxaca, Mexico. The range extends in a generally north-northeast to south-southwest direction, but the section from Cofre de Perote to Loma Alta extends mainly east-northeast and has been straightened. This mountain system is home to 17 described and several unnamed species of minute salamanders, genus *Thorius*. Most of the species are clustered between 1,500 and 3,000 m. All of the species that have been evaluated are Endangered (E) or Critically Endangered (CR) and at risk of extinction, and three have been found so infrequently that they are categorized as Data Deficient (DD) (Global Amphibian Assessment, 2007).

a little above that level. Of the 17 named species, 11 are listed as Endangered and 3 are listed as Critically Endangered; the remaining 4 species are so rare and poorly known that they can only be listed as Data Deficient (Fig. 2.4) (SN Stuart *et al.*, 2004). We consider this region to be a hot spot of extinction, and yet it is still very incompletely known. Based on our studies of altitudinal transects elsewhere in Middle America, we expect that the situation we have described for eastern Mexico is typical of mountainous parts of the entire region.

WHAT WILL WE LOSE?

The amphibians at greatest risk of extinction are likely to be those with relatively few populations in areas undergoing rapid habitat conversion because of human activities. Populations that are already reduced in size are especially susceptible to other stressors, such as introduced species and disease. Tropical montane species are at special risk because of global warming. These already stressed species, reduced to a few populations, also are likely to be hit hardest by Bd. However, a paradoxical fact is that new species of amphibians are being described at an unprecedented rate. In 1985, the first comprehensive account of all amphibian species reported ≈4,000 species (Frost, 1985). That number has now risen to >6,300, and species are being named at a rate exceeding 2% per year. Some of these species are cryptic forms that were found as a result of molecular systematic studies, but the vast majority are morphologically distinctive species mainly from tropical regions (Fig. 2.5). These biologically unique species often have been found as a byproduct of the heightened interest in amphibians and consequent field research. Field surveys in still relatively unstudied parts of the world (e.g., New Guinea and nearby islands, Madagascar) have resulted in many new discoveries. Among the most spectacular discoveries during this decade are a frog from India that is so distinct that it was placed in a new family (Biju and Bossuyt, 2003) and a salamander from South Korea that is the only member of the Plethodontidae from Asia (Min *et al.*, 2005). It is impossible to know what has been overlooked or has already been lost to extinction, but there is every reason to think that the losses have been substantial.

The rate of extinction of amphibians is truly startling. A recent study estimates that current rates of extinction are 211 times the background extinction rate for amphibians, and rates would be as high as 25,000–45,000 times greater if all of the currently threatened species go extinct (McCallum, 2007).

Despite these alarming estimates, amphibians are apparently doing very well in many parts of the world, and many thrive in landscapes heavily modified by human activities. Species such as the cane toad (*Bufo marinus*), the American bullfrog (*Rana catesbieana*), and the clawed frog (*Xenopus laevis*) have proven to be potent invasive species, and they have not yet been shown to be afflicted by chytridiomycosis. Attempts are being made to mitigate anticipated losses of amphibian species. Promising research on bacterial skin symbionts of amphibians suggests that they may have antifungal properties (Harris *et al.*, 2006; Woodhams *et al.*, 2007), possibly opening pathways for research on changing the outcomes of fungal attacks. Local extinctions have been so profound and widespread in Panama that a major initiative has been launched to promote *in situ* as well as *ex situ* captive breeding programs. Species will be maintained in captivity until solutions to problems such as chytridiomycosis, local habitat destruction, or others can be mitigated, at which time reintroduction programs will be developed (Gewin, 2008). Although amphibians are suffering declines and extinctions, we predict that at least some frogs,

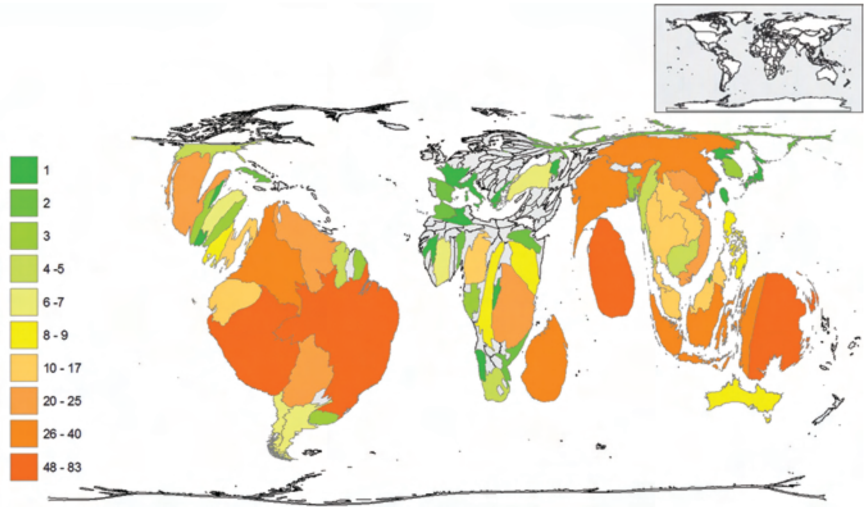

FIGURE 2.5 Distribution of species of amphibians discovered and named during the period 2004–2007. Bar indicates number of new species per country. (*Inset*) Baseline world map. Visualization is based on density-equalizing cartograms prepared by M. Koo.

salamanders, and caecilians will survive the current extinction event on their own or with help, even as their ancestors survived the four preceding mass extinctions.

WHAT IS THE PRINCIPAL CAUSE OF THE PRESENT EXTINCTION SPASM?

Human activities are associated directly or indirectly with nearly every aspect of the current extinction spasm. The sheer magnitude of the human population has profound implications because of the demands placed on the environment. Population growth, which has increased so dramatically since industrialization, is connected to nearly every aspect of the current extinction event. Amphibians may be taken as a case study for terrestrial organisms. They have been severely impacted by habitat modification and destruction, which frequently has been accompanied by use of fertilizers and pesticides (Hayes *et al.*, 2002). In addition, many other pollutants that have negative effects on amphibians are byproducts of human activities. Humans have been direct or indirect agents for the introduction of exotic organisms. Furthermore, with the expansion of human populations into new habitats, new infectious diseases have emerged that have real or potential consequences, not only for humans, but also for many other taxa, such as the case of Bd and amphibians (Cunningham *et al.*, 2006). Perhaps the most profound impact is the human role in climate change, the effects of which may have been relatively small so far, but which will shortly be dramatic (e.g., in the sea) (Jackson, Chapter 1, this volume). Research building on the Global Amphibian Assessment database (SN Stuart *et al.*, 2004) showed that many factors are contributing to the global extinctions and declines of amphibians in addition to disease. Extrinsic forces, such as global warming and increased climatic variability, are increasing the susceptibility of high-risk species (those with small geographic ranges, low fecundity, and specialized habitats) (Sodhi *et al.*, 2008). Multiple factors acting synergistically are contributing to the loss of amphibians. But we can be sure that behind all of these activities is one weedy species, *Homo sapiens*, which has unwittingly achieved the ability to directly affect its own fate and that of most of the other species on this planet. It is an intelligent species that potentially has the capability of exercising necessary controls on the direction, speed, and intensity of factors related to the extinction crisis. Education and changes of political direction take time that we do not have, and political leadership to date has been ineffective largely because of so many competing, short-term demands. A primary message from the amphibians, other organisms, and environments, such as the oceans, is that little time remains to stave off mass extinctions, if it is possible at all.

ACKNOWLEDGMENTS

We thank M. Koo for producing Figs. 2.1, 2.2, and 2.5 [using methods from Gastner and Newman (2004) and data from SN Stuart *et al.* (2004), AmphibiaWeb (2007), and Global Amphibian Assessment (2007)]; K. Klitz and R. Diaz for help with Fig. 2.4; colleagues who aided in collecting and analyzing data; C. Briggs, R. Knapp, and T. Tunstall (Sierra Nevada) and M. Garcia-Paris, G. Parra-Olea, and J. Hanken (Mexico) for discussion; J. Avise and J. Jackson for comments on this manuscript; and M. H. Wake for a thorough review of the manuscript and extensive discussion. This work was supported by National Science Foundation Grant EF0334939 (to D.B.W.) and National Institutes of Health/National Science Foundation Ecology of Infectious Disease Program Grant R01ES12067 [to C. Briggs (University of California, Santa Barbara)].

3

Patterns of Biodiversity and Endemism on Indo-West Pacific Coral Reefs

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and ALEXEI U. KUDLA†

Diversity of the primary groups of contemporary Indo-West Pacific coral reef organisms, including mantis shrimps (stomatopod crustaceans), peaks in the Indo-Australian Archipelago (IAA), reaches a lower peak in East Africa and Madagascar [Indian Ocean continental (IOC)], and declines in the central Indian Ocean (IO) and Central Pacific (CP). Percent endemism in stomatopods (highest in the IAA, high in the IOC, lower in regions adjacent to centers, and moderate in the CP) correlates positively with species diversity (this varies with scale) and inversely with species body size. Because it constrains reproductive traits and dispersal, body size is a reliable indicator of speciation and extinction potential in reef stomatopods and probably most marine organisms. Assemblages are dominated by small-sized species in the IAA and IOC. Both speciation and extinction likely are high, resulting in especially high endemism (small ranges reflect both originating and disappearing species) in these regions. Rates of speciation exceed extinction, yielding centers of diversity (especially in the IAA). Dispersal slows speciation and extinction in areas adjacent to these centers. Body size declines toward the CP, especially in atoll environments. Here the wheels of speciation and extinction again spin rapidly but in the opposite direction (extinction > speciation),

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yielding low diversity and moderate endemism. We conclude that life histories, dispersal, and speciation/extinction dynamics are primary agents that mold patterns of diversity and endemism. Historical factors, currents, productivity, and species diversity itself (through ecological interactions) also influence these patterns, in some cases by altering body size.

Being repositories of ancient phyla as well as more recent specialized taxa, coral reefs are among the most spectacular, productive, diverse (per unit area), and threatened ecosystems on Earth. Organisms they house provide a critical source of protein for people in many tropical countries, and reefs themselves protect human populations from storm and wave damage. Coral reefs provide aesthetic beauty (and the bioeroded sand on beaches) for tourism—an increasingly important economic resource for developing tropical countries. However, tourism and other uses of reefs must be carefully managed to be of sustainable economic benefit. A fundamental value of coral reefs is that they provide an aesthetic, intellectual, educational, and cultural heritage for present and future generations.

Threats to global coral reefs, however, are severe and well documented (Bryant *et al.*, 1998; Burke *et al.*, 2002; Gardner *et al.*, 2003; Hughes *et al.*, 2003; Pandolfi *et al.*, 2003, 2005; Bellwood *et al.*, 2004; Burke and Maidens, 2004; Hoegh-Guldberg *et al.*, 2007). Overexploitation has been identified as an especially serious problem, but other threats include coastal development and sedimentation, pollution, global warming, disease, and ocean acidification. The Global Coral Reef Monitoring Network reports that 20% of global coral reefs already have been degraded beyond recovery, an additional 24% are under imminent threat of collapse, and a further 26% are at longer-term risk (Wilkinson, 2004). In the Indo-West Pacific (IWP), 88% of Southeast Asian reefs and 61% and 54% of Middle Eastern and Indian Ocean (IO) reefs are at medium to high risk (Bryant *et al.*, 1998; Burke *et al.*, 2002). Human population density near reefs is particularly high in Southeast Asia and the IO. Pacific reefs are in better condition (59% at low risk), with more protected area, than those in other regions.

Despite the biological, cultural, and economic value of coral reefs and the widely publicized alarm at their global decline, it remains astonishing how little we know about the patterns of diversity ("diversity" will be used equivalently to species richness) on coral reefs that would help us manage and conserve them. This chapter will (*i*) review and provide new information on the geography of coral reef diversity in the IWP using information from the most ecologically important and well-known groups of reef organisms, (*ii*) provide a brief overview of the major factors that generate these patterns, and (*iii*) briefly review "hotspots" and provide new information on endemism in reef stomatopods. (*iv*) We will then examine information on body size, life history characteristics, geographic ranges, and speciation/extinction dynamics of reef stomatopods and other organisms to suggest mechanisms that, in combination with environmental factors, can explain the observed patterns of IWP coral reef diversity and endemism.

We will focus on reef-dwelling mantis shrimps as a model taxonomic group for such analyses because these crustaceans are important members of the benthic community. All stomatopods are predators with a pair of enlarged, equally sized raptorial claws that are used to smash and spear prey, competitors, and predators (Fig. 3.1). Protective holes in the substrate are a limiting resource because of strong fish predation; stomatopods exhibit colorful communicatory displays and intense territorial fighting to maintain exclusive ownership of these holes (Caldwell and Dingle, 1975; Reaka and Manning, 1981).

PATTERNS OF CORAL REEF DIVERSITY

Species diversity for several marine taxa (fishes, corals, lobsters, and snails) reaches a global maximum in the "East Indies triangle" (Malaysia, Indonesia, New Guinea, and the Philippines) of the Indo-Australian Archipelago (IAA), declines in the IO (with heightened diversity in some parts of the western IO for many taxa), declines eastward across the Central Pacific (CP), and peaks again in the Caribbean (Steli and Wells, 1971; Briggs, 1995, 1999a, 2000, 2003, 2007; Veron, 1995; Paulay, 1997; Bellwood and Hughes, 2001; Hughes *et al.*, 2002; Roberts *et al.*, 2002; Meyer, 2003; Mora *et al.*, 2003; Bellwood *et al.*, 2005). The first diversity contour map for reef stomatopods (Fig. 3.2) shows a similar pattern, with a high, sharp peak in the central IAA and an area of elevated diversity in the northwestern IO that increases southward to a secondary peak around Madagascar. Similar to most other taxa where contours of diversity are known, tails of diversity extend from the IAA toward the southeast and northeast.

EXPLANATIONS OF IWP DIVERSITY GRADIENTS

After considering all explanations for patterns of IWP reef biodiversity, we identify here only those that are most applicable to the present study.

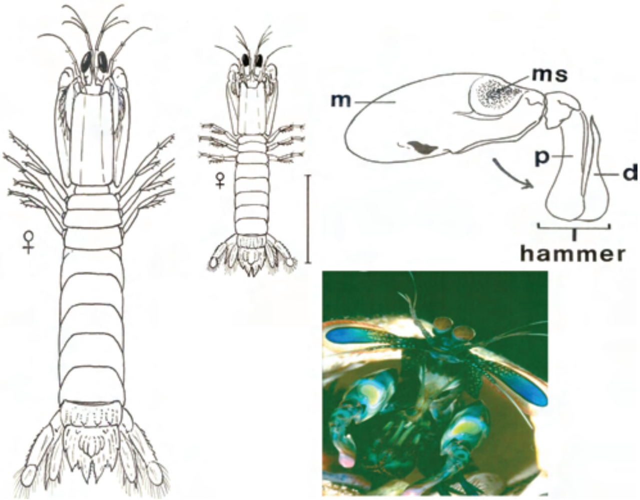

FIGURE 3.1 Dorsal view of typically sized reef stomatopods (large *Gonodactylaceus falcatus*, small *Gonodactylellus incipiens*; scale bar for both is 10.0 mm), lateral view of raptorial claw, and photograph of individual delivering a threatening display at the entrance of its burrow (*Gonodactylaceus ternatensis*, courtesy of Roy Caldwell). Drawing of the raptorial claw shows the merus (m), meral spot (ms, which varies in color from white through yellow, orange, red, pink, purple, and blue among species), propodus (p), and dactyl (d); p and d normally are folded against m but are opened (arrow) either together as a hammer or with d projected as a spear. Coloration of the flared antennal scales and setae also varies from yellow to red, blue, and green among species.

Faunal Carryover Hypothesis

Species from a Mesozoic/early Cenozoic center of diversity in Europe migrated east to the IAA and probably south along the continental margin of the Indian Ocean (IOC) as the Tethys Seaway was closed by the collision of Africa with Eurasia between the Paleocene and Miocene (Briggs, 2000, 2003, 2007). High stomatopod diversity in the IAA and in the western/southwestern IO (Fig. 3.2) is consistent with this hypothesis.

Center of Accumulation Hypothesis

Species originate in small peripheral populations, larvae from peripheral regions are carried by currents into central areas favorable for reef growth (arrows in Fig. 3.2), and species accumulate in these current-fed

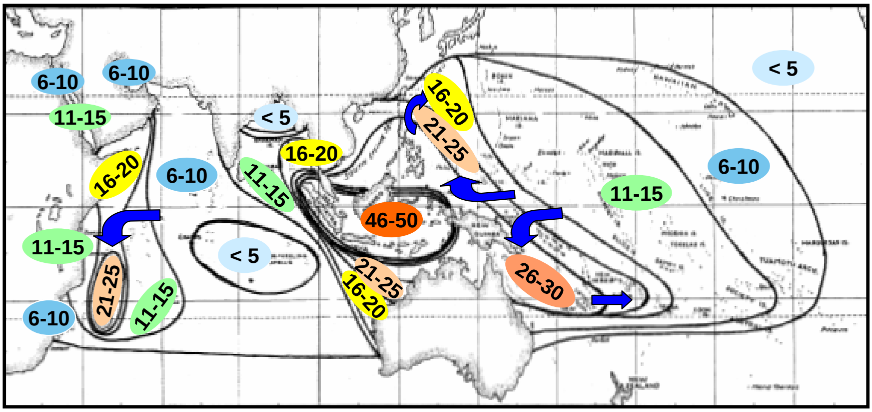

FIGURE 3.2 Contours of species richness for reef stomatopods in the IWP. Numbers represent species present in each contour. Arrows indicate major currents. All species of Alainosquillidae, Gonodactylidae, Odontodactylidae, Protosquillidae, and Takuidae are included; Pseudosquillidae occur on reefs but are excluded from analysis because their reproductive, larval, and life history patterns differ from those of other reef-dwelling families (Reaka, 1979, 1980; Reaka and Manning, 1987a). Data are from our own collections, National Museum of Natural History collections, and published literature [updated to currently accepted taxonomy (Ahyong, 2001; Schram and Muller, 2004)].

regions over time (Ladd, 1960; Jokiel and Martinelli, 1992; Briggs, 1995; Connolly *et al.*, 2003). Peaks of stomatopod diversity in the IAA and western IO are consistent with this hypothesis, but Barber and Bellwood (2005) and the present study find speciation and endemism in both peripheral regions and diversity centers.

Energy/Productivity Hypothesis

Higher productivity—the rate at which energy flows through an ecosystem—allows an ecosystem to support more species (although diversity often declines at very high levels of productivity) (Rosenzweig, 1995). Similarly, increased temperature accelerates speciation (Allen and Gillooly, 2006; Allen *et al.*, 2006), but Bellwood *et al.* (2005) find no relationship between sea surface temperature and diversity of reef corals and fishes. Phytoplankton abundance has not been compared previously with contours of reef diversity. The general pattern of stomatopod diversity correlates fairly well with phytoplankton productivity (Figs. 3.2 and 3.3). We later infer that phytoplankton productivity affects body size and extinction/speciation dynamics of stomatopods on high (volcanic peaks with

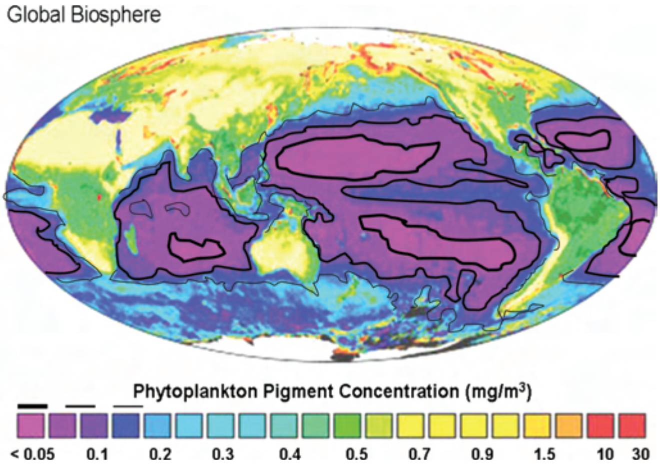

FIGURE 3.3 Distribution of global phytoplankton pigment concentration (adapted with permission from the National Aeronautics and Space Administration). Among reef areas, phytoplankton pigments are particularly abundant (0.3–0.4 mg/m^3) off the Arabian Peninsula and west coast of India/Sri Lanka, around the Malay Peninsula/Indonesia, and around New Guinea/northern Australia. Pigment concentrations decline to 0.15 mg/m^3 in a relatively narrow band oceanward from the above areas; immediately offshore from the continental margin of western Australia, eastern Africa, Madagascar; and in an equatorial band extending westward from the central East Pacific. Still further offshore, phytoplankton pigments decline (0.05 mg/m^3) until they reach the very low levels characteristic of the centers of the northern and southern gyres of the Indian and Pacific Oceans (<0.05 mg/m^3, smallest oceanic circles). We drew black lines for each of these contours by eye from map coloration.

extensive terrestrial area and soil) vs. low (carbonate atolls with little elevation or nutrient runoff) mid-Pacific islands. The fact that terrestrial runoff elevates productivity around high vs. low Pacific islands, enhancing the survival of phytoplankton-feeding starfish larvae and fostering crown of thorns starfish population explosions (Birkeland, 1982; Brodie *et al.*, 2005; Houk *et al.*, 2007), suggests that productivity can have important effects on larval recruitment, local reef populations, and hence reef biodiversity.

Center of Origin Hypothesis

"Successful" lineages originate in the East Indies; species subsequently migrate into peripheral regions, where they remain as relicts; gaps in species distributions suggest high extinction as well as origination in the East

Indies (Briggs, 1995, 1999a,b, 2000, 2003, 2007). Although much evidence supports this hypothesis, species of reef fish are not consistently young in the IAA and old in peripheral regions (Barber and Bellwood, 2005), and the present study suggests that, in reef stomatopods, both speciation and extinction are high in peripheral areas as well as in the IAA.

Species Diversity Hypothesis

High species diversity itself may promote diversification [Emerson and Kolm (2005), but see Cardena *et al.* (2005)], probably through species interactions. Speciation rates in three groups of fossil plankton over 2–20 Myr correlate with species diversity independent of sampling intensity and area (Allen and Gillooly, 2006). In the present study, species interactions in diverse assemblages may cause shifts in body size and consequent changes in life history patterns and speciation/extinction patterns.

Life History Speciation/Extinction Hypothesis

We will suggest that the biotic and environmental processes that govern body size and life history traits drive rates of speciation/extinction and thus patterns of diversity in IWP stomatopods and other reef organisms.

ENDEMISM AND HOTSPOTS

Endemism has been of particular interest as an indicator of extinction. The concept of biodiversity hotspots—concentrations of endemic species that are at exceptional risk—was motivated by the need to establish conservation priorities (Myers, 1988; Reid, 1998; Myers *et al.*, 2000; Mittermeier *et al.*, 2004). However, some authors have argued that high overall diversity or phylogenetically unique taxa or habitats deserve priority attention, and others have shown that centers of endemism do not always coincide among taxa or with degree of threat (Prendergast *et al.*, 1993; Williams *et al.*, 1996; Bonn *et al.*, 2002; Orme *et al.*, 2005). For some of the same reasons, hotspots on global coral reefs have been controversial (Baird *et al.*, 2002; Briggs, 2002; Hughes *et al.*, 2002; Roberts *et al.*, 2002). Here we examine patterns of endemism in the context of both speciation and extinction, because limited ranges occur during both processes. Conservation of areas rich in endemics is important not only because they are at particular risk of species loss but also because they represent potential sources of diversification.

Endemism in reef stomatopods varies with scale. When stomatopods are known from only a single locality, these "local endemics" are widely scattered (Fig. 3.4), with no significant relationship between number of

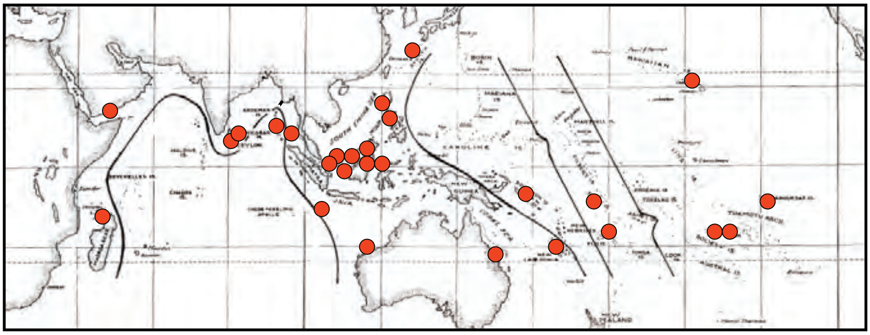

FIGURE 3.4 "Locally endemic" species of reef stomatopods.

endemics and number of species found at each local site ($x^2 = 12.72$, df = 20, $P > 0.05$). Average endemism for the 21 local sites is 10.5 ± 2.6% (SE).

"Restricted regional endemics"—those known from local sites, archipelagos, and parts of regions—are widespread but reach their highest incidences (>15%) in the Malay Peninsula/Indonesia/Philippines, Red Sea, Mascarene Islands, Madagascar/Comores Islands, Society Islands, and Hawaiian Islands (Fig. 3.5). However, the distribution of restricted regional endemics does not differ from those expected when the diversities of their subregional stomatopod faunas are considered ($x^2 = 25.13$, df = 23, $P > 0.05$). Endemism across the 24 subregions averages 14.5 ± 2.1%.

To examine patterns of endemism at a larger scale, the IWP was divided into major "regions" of continental and oceanic habitat types. At this scale, percent endemism (squares) is significantly concentrated in the IAA and drops in the adjacent oceanic regions but then rises toward the

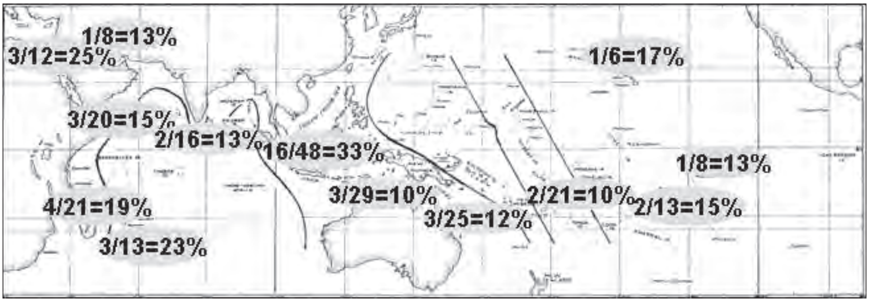

FIGURE 3.5 "Restricted regional endemic" species of reef stomatopods. Of the 24 subregions considered, those that exceed 10% are shown.

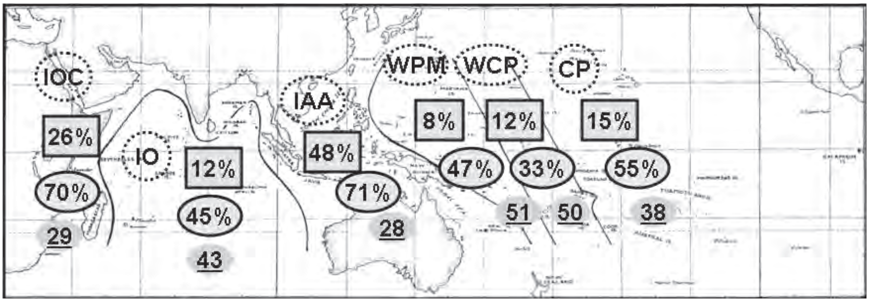

FIGURE 3.6 Endemism and body size of reef stomatopods in six different regions (dashed circles) consisting of the IOC, IO, IAA (the western margin of the IAA abuts the IOC off Burma), Western Pacific margin (WPM), West Central Pacific (WCP), and CP. Numbers in each region represent (*i*) percentage of species in each region that are endemic (square, top number in each region; percentage is used to avoid confounding diversity with endemism and because the regions are not equal in area), (*ii*) percentage of species in each region <40 mm in body length (oval, middle number in each region; 40 mm is the median body size across all regions), and (*iii*) median body size (millimeters total length) among species in each region (underline bar, bottom number in each region).

west in the IOC and, to a lesser extent, toward the east in the West Central Pacific and especially the CP ($x^2 = 26.23$ using raw numbers of endemics/nonendemics, df = 5, $P < 0.001$; Fig. 3.6). Average endemism among the six regions is 20.2 ± 6.1%.

The percent regional endemism increases significantly with regional species richness (Fig. 3.7; $r^2 = 0.74$, $P = 0.03$, $F = 11.41$, $y = 0.08x + 1.61$, square-root-transformed data).

The percent regional endemism is inversely related to body size among regions, decreasing with increased median body size (Fig. 3.7; $r^2 = 0.65$, $P = 0.05$, $F = 7.53$, $y = 0.10x + 8.16$, square-root-transformed data) and increasing with percentage of species in each region that are <40 mm in body size ($r^2 = 0.68$, $P = 0.04$, $F = 8.39$, $y = 0.08x - 0.15$, square-root-transformed data).

Species are concentrated in small body size classes in the IAA and IOC, although the range of body sizes is large in these regions. Typical body sizes are larger in the oceanic regions adjacent to the IAA and IOC but decline (with an absence of large-sized species) toward the CP (Fig. 3.6; number of species >40 mm and <40 mm for all regions, $x^2 = 11.07$, df = 5, $P = 0.02$).

Hypothesizing that productivity influences body sizes and life histories of reef stomatopods, we further categorized the species in the six regions according to whether they inhabited productive or unproductive

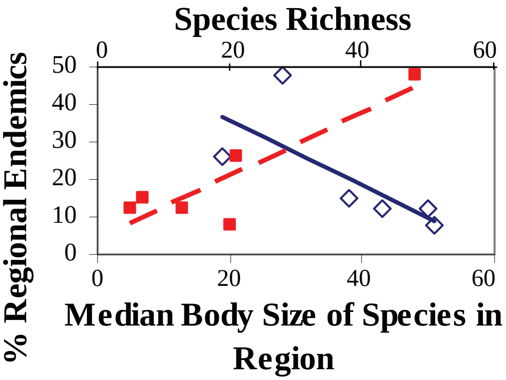

FIGURE 3.7 The percentage of regional endemics vs. median body size of species in each region (open diamonds) and species richness in each region (filled squares) for reef stomatopods. Residual analyses show no difference in and statistical results are similar for transformed and untransformed data; untransformed data are shown here.

environments. Because of terrestrial runoff, continental regions and high islands are expected to have higher nearshore productivity than low oceanic islands. Analysis of maximal species' body sizes on continental and high vs. low island environments shows, as above, that endemism is consistently associated with small body size ($F = 39.27$, df = 157, $P < 0.001$, type 3 ANOVA tests of fixed effects for regional endemism, terrain height, and region, log-transformed data; analysis using species median body size yields the same result). Terrain height is not consistently related to body size across all six regions, probably because of the large species scattered throughout the IOC, IO, and IAA (type 3 ANOVA of fixed effects as above, $P > 0.05$; for number of species >40 mm and <40 mm on continental/high vs. low islands across the region, $x^2 = 15.3$, df = 9, $P = 0.08$). However, a previous study of reef stomatopods showed that body size of individual populations within each of four species complexes of reef stomatopods declines significantly from the IAA toward the CP and that populations on high islands reach significantly larger body sizes than those inhabiting atolls in these regions (Reaka-Kudla, 2000). Guided by the previous study, we analyzed maximal and median body sizes of species assemblages from high vs. low islands from the West Central Pacific and CP. High islands support species of significantly larger body size than low islands in these regions ($F = 4.79$, df = 40, $P = 0.03$; type 3 ANOVA of fixed effects for region, island height, and regional endemism, log-transformed data; analysis of median body size of species yields a similar result).

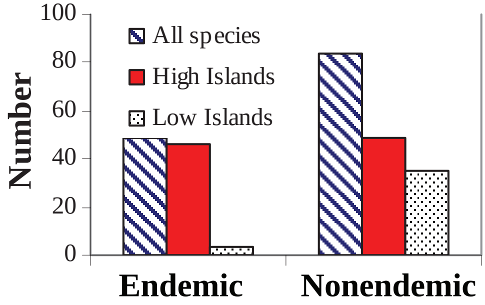

FIGURE 3.8 Number of regional endemic vs. nonendemic species of reef stomatopods and those occurring on high vs. low islands.

Number of endemics and nonendemics on high vs. low islands did not vary significantly across regions ($P > 0.05$), so all regions were combined. Significantly fewer endemics occur on low than high islands ($x^2 = 19.16$, df = 1, $P < 0.001$; Fig. 3.8).

LIFE HISTORY PATTERNS OF REEF STOMATOPODS

We propose that the ecological and environmental factors that govern body size and life history traits drive patterns of diversity and endemism in reef organisms. Large body size in reef stomatopods is significantly correlated with massive reproductive output (more and larger eggs; Figs. 3.9 and 3.10), greater planktonic larval dispersal, larger geographic ranges, and greater saturation of available reef habitat within ranges (Fig. 3.11), whereas small body size correlates with restricted reproductive capacity, restricted larval dispersal, and relative rarity (low abundance, few sites, small geographic ranges) (Reaka, 1979, 1980; Reaka and Manning, 1987a; Reaka-Kudla, 1991; Wilkinson, 2004). This correlation occurs because small body size constrains reproductive traits in marine organisms. Small-bodied species cannot produce enough small plankton-feeding larvae to leave one surviving offspring given the high mortality rate suffered by these long-lived larvae. Small species must endow fewer, larger larvae with yolk supply, often brooding them before a relatively brief planktonic period, to increase survivorship. The body volume of larger species allows them to produce sufficient numbers of small larvae that feed in the plankton for long periods that some offspring survive despite heavy mortality (Menge, 1975; Strathmann and Strathmann, 1982). Size frequency distributions for both body size (Fig. 3.12) and geographic range (Fig. 3.13) are strongly shifted toward diminutive sizes (particularly in endemic species) and

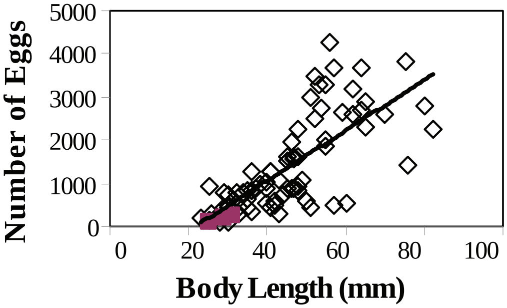

FIGURE 3.9 Egg number per individual increases significantly with body size among species of gonodactylid (open diamonds) and protosquillid (filled squares) reef stomatopods ($r^2 = 0.55$, $F = 92.74$, $P < 0.001$, $y = 58.71x - 1291.69$).

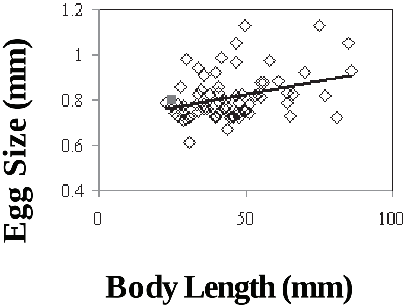

FIGURE 3.10 Mean egg size per individual increases significantly with body size among species of gonodactylid (open circles) and protosquillid (closed square) reef stomatopods ($r^2 = 0.12$, $F = 9.45$, $P = 0.003$, $y = 0.002x + 0.71$).

restricted distributions in reef stomatopods. The latter indicates that most reef stomatopods risk extinction if faced with rapid global environmental changes.

Life history patterns of stomatopods are consistent with those found in other living and fossil groups for reproductive and life history traits, patterns of abundance, and frequency distributions of body size and geographic range. Body size is positively correlated with fecundity and colonizing ability in most marine invertebrates (Reaka, 1979, 1980; Strathmann and Strathmann, 1982; Jablonski and Lutz, 1983; Strathmann, 1985, 1990; Jablonski, 1986b, 1996; Reaka-Kudla, 1991; Roy *et al.*, 2001, 2002; Jablonski

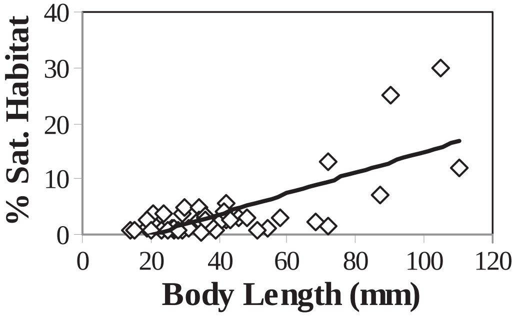

FIGURE 3.11 The percentage saturation of available reef habitat within each species' geographic range increases significantly with median body size among species of gonodactylid and protosquillid stomatopods ($r^2 = 0.54$, $F = 47.68$, $P < 0.001$, $y = 0.19x - 3.83$). The percentage saturation of each species' range is the proportion of all 5 × 5° latitudinal and longitudinal quadrants containing habitable reef that is occupied by that species.

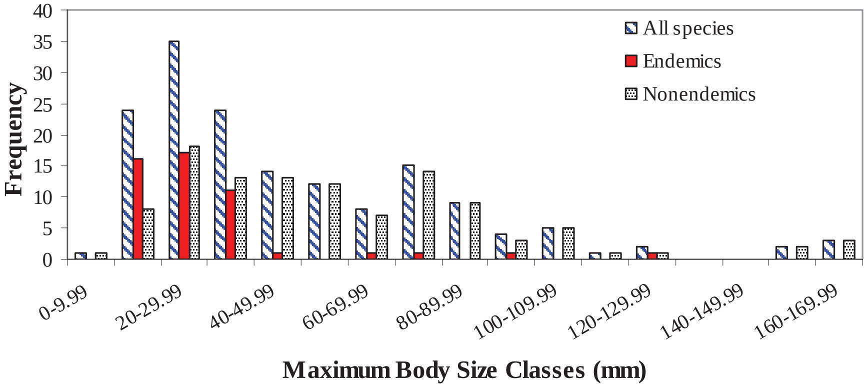

FIGURE 3.12 Size frequency distributions of maximum body sizes for total species, regional endemics, and nonendemic species of reef stomatopods. Endemics are significantly smaller than nonendemics ($t = 6.40$, df = 146, $P < 0.001$; two-sample t test assuming unequal variance). Analysis of median body size for each species gives a similar graphical and statistical result.

et al., 2003a). Stomatopods share the following characteristics with taxa in both marine and terrestrial environments. (*i*) Body size frequency distributions are usually shifted toward small size classes (May, 1978, 1986, 1988; Rosenzweig, 1995; Gaston and Blackburn, 2000; Roy *et al.*, 2000, 2002). (*ii*) Species abundances are biased toward few common and many rare species (Hubbell, 2001). (*iii*) Local abundance increases with range size (Gaston, 1994). (*iv*) Geographic range size increases with body size

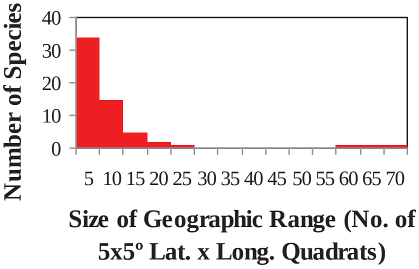

FIGURE 3.13 Size frequency distribution of geographic ranges in reef stomatopods (Lat, latitude; Long, longitude). Other measures of geographic range size [latitudinal distance, longitudinal distance, square root of (latitude × longitude)^2] yield a similar plot.

(Gaston and Blackburn, 1996). (*v*) Frequency distributions for geographic ranges are shifted toward small ranges [Gaston (1994, 1998), Gaston and Chown (1999), and Roberts and Hawkins (1999), but see Hughes *et al.* (2002)]. Commonalities in patterns of body size, life history, and distribution between reef stomatopods and other taxa suggest that the relationship between life history mechanisms and patterns of diversity and endemism we find in benthic reef organisms also may operate in other systems.

SPECIATION AND EXTINCTION

Factors that influence the relative rates of speciation vs. extinction control the geography of species diversity and endemism. This section will review briefly some of the factors thought to determine rates of extinction and speciation in marine and other organisms, and *Discussion* will apply these generalities to the patterns of diversity and endemism observed in IWP reef stomatopods.

Species or genera that are widespread, abundant, and dispersive resist extinction in both marine and terrestrial environments and both fossil and contemporary lineages (Jablonski, 1986a,b, 1987, 1991; Gaston, 1994; Hubbell, 2001; Jablonski *et al.*, 2003a). In addition to geographic range, which is sufficient on its own to explain species survival (Jablonski and Hunt, 2006), the presence of long-lived larvae and species richness of the clade confer resistance to background extinction in fossil marine bivalves (Jablonski, 1986a, 1991). Broad distribution of the clade confers protection against mass extinction (Jablonski, 1986a, 1991, 2007; Powell, 2007a). In addition, latitudinal distribution affects extinction, with the tropics—especially reef faunas—being subject to repeated upheaval, particularly during mass extinctions (Jablonski, 1991, 1993; Powell, 2007b).

In stomatopods, evidence of extinction is derived from conspicuous gaps in regional distributions. For example, when a lineage occurs in the IWP, East Atlantic, and East Pacific but is absent from the West Atlantic, the most parsimonious explanation, given what is known about Cenozoic extinctions in the Americas (Jackson *et al.*, 1996; Budd, 2000; Jackson and Johnson, 2000; Todd *et al.*, 2002), is that it became extinct in the West Atlantic. Such "apparent extinctions" are significantly elevated in lineages with restricted dispersal and small ranges as well as those from coral reefs and tropical latitudes (Reaka and Manning, 1987a). Although adult body size is not significantly associated with such gaps, small body size correlates significantly with reduced larval dispersal and small geographic ranges and can be used as an indicator of extinction risk (Reaka, 1980; Reaka and Manning, 1987a).

Speciation also is related to life history characteristics and geographic range size. Although the relationship between geographic range size and speciation has been debated (Rosenzweig, 1995; Chown, 1997; Gaston, 1998; Gaston and Chown, 1999; Jablonski, 2007), range size is positively related to dispersal ability and gene flow in many marine and terrestrial taxa (Reaka, 1980; Reaka and Manning, 1981, 1987a; Jablonski and Lutz, 1983; Jablonski *et al.*, 2003a; Paulay and Meyer, 2006), and these factors tend to dampen rates of speciation (Mayr, 1963; Hubbell, 2001; Jablonski *et al.*, 2003a). Paleontological approaches allow measurement of both speciation rates and geographic range sizes over time. Range size is significantly inversely related to speciation rates in fossil gastropods and brachiopods (Jablonski and Roy, 2003; Jablonski *et al.*, 2003a; Jablonski, 2007; Powell, 2007b).

Because it constrains reproductive traits and geographic range, body size can be used as an indicator of speciation rate. Evidence that small-bodied species are engines of diversification comes from studies of morphological and taxonomic divergence of stomatopod lineages across biogeographic barriers (Reaka and Manning, 1981, 1987a). Large-bodied lineages and those with long-lived larvae remain conspecific (morphologically indistinguishable) or closely related (cognate species) when separated by a barrier (e.g., the Central American isthmus) significantly more frequently than small-bodied species with abbreviated larval development. Conversely, the percentage of endemic species without cognates elsewhere and the percentage of species within locally radiating clusters of species (more closely related to each other than to any species outside the region) are significantly elevated in lineages of small body size, of limited larval dispersal, and from reefs.

Recent molecular studies, including those on gastropods and small-bodied stomatopods, show that incipient or full speciation is more common in reef fauna than previously thought (Barber *et al.*, 2000, 2002, 2006;

Meyer, 2003; Meyer *et al.*, 2005). In addition to the fact that most benthic reef species are small in body size (Reaka-Kudla, 1997; Bouchet *et al.*, 2002; Meyer *et al.*, 2005) with restricted or moderate colonizing ability, the behavior of reef larvae further reduces dispersal. Stomatopod larvae (and those of most other reef taxa) exhibit diurnal vertical migrations, hiding in reef rubble by day and migrating into the water column at dusk and dawn (Robichaux *et al.*, 1981), which reduces exposure to currents. Although panda clownfish have a 9- to 12-day pelagic phase, one-third of marked juveniles settle within their natal area, many within 100 m of their birth site (GP Jones *et al.*, 2005).

DISCUSSION

Using body size as an indicator of speciation and extinction rates, we infer that the IAA, and to a lesser extent the IOC, are areas of both high origination and high extinction in reef stomatopods. However, rates of origination must exceed those of extinction in these areas, yielding the high biodiversity observed. Endemism results from either newly originated or almost extinct species and thus is expected to be especially high if both speciation and extinction are elevated, as is observed. Although species are concentrated in small size classes in the IAA and IOC, the range of body sizes is large in these areas (see Fig. 3.14). Historical factors (faunal carryover from the Tethys Seaway), productivity in the continental areas, currents, and species diversity itself (via ecological interactions between species) likely have contributed to the species richness and range of body sizes in the IOC and IAA. The dispersal and colonizing capability of large-sized species in these areas allows them to disproportionally colonize adjacent oceanic regions, where extensive larval immigration lowers extinction and retards speciation, yielding moderately diverse, somewhat larger-sized assemblages with low endemism.

In the center of the IO and in the broader expanse of the Pacific, however, larval immigrants have been filtered by starvation, predation, and distance. Given enough time, it is likely that larvae from diversity centers reach mid-ocean islands. However, both diversity and adult body size of reef stomatopods decline in the mid-Pacific, and body size is smaller on mid-Pacific atolls than on high islands, suggesting that productivity of the island environment, as well as propagule pressure, influences successful colonization. Dwarfed by limited productivity, populations cannot produce sufficient propagules to reach another island archipelago and are unlikely to receive many immigrants from ancestral populations to the west. They diverge into new species; endemism increases toward the CP. However, extinction also must be exceedingly high in these small-sized peripheral species. Endemics are missing from atolls, probably reflect-

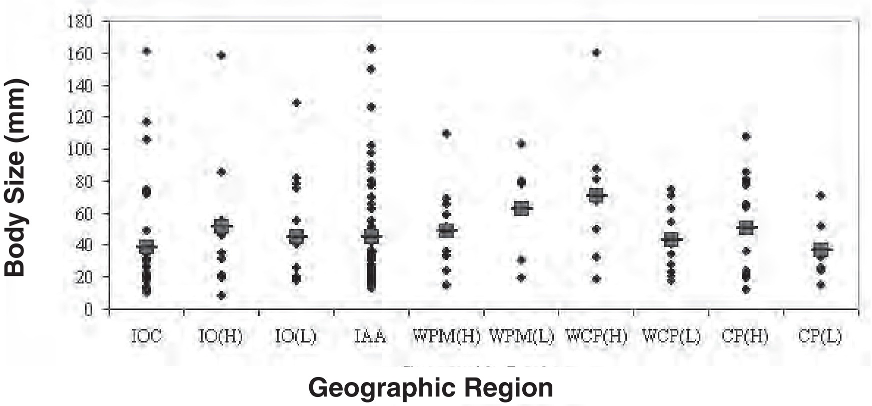

FIGURE 3.14 Body sizes of species on continental and high vs. low islands from the IOC to the CP. (H) and (L) refer to high and low island environments. Regional abbreviations are as in Fig. 3.6. Data for each species represent maximal recorded body length; plots for median body length provide a very similar pattern. Squares with crossbars are means.

ing the difficulty of establishing successful populations in these low-productivity environments that are heavily dominated by top predators (M.L.R., personal observation). We have observed one instance of population extinction in a small-sized reef stomatopod from a mid-Pacific atoll (Reaka and Manning, 1987b). Consequently, the wheels of speciation and extinction turn rapidly, but in reverse direction. If species arrive, speciation is high but extinction even higher; thus, diversity is low in remote oceanic regions of the IO and CP. Although the available evidence from life histories, geographic ranges, and extinction/speciation in stomatopods and other organisms supports this interpretation, molecular evidence on ages of species also is needed.

We conclude that life history patterns and dispersal are the primary mediators of the rate and direction of the speciation/extinction cycle, which in turn determines the geography of diversity and endemism. However, productivity, historical factors (antecedent faunas), and currents likely influence diversity in particular localities. In addition, productivity, historical factors (lineage history), and species diversity itself (through ecological interactions) alter body size and thus influence life history and dispersal.

ACKNOWLEDGMENTS

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4

Homage to Linnaeus: How Many Parasites? How Many Hosts?

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Estimates of the total number of species that inhabit the Earth have increased significantly since Linnaeus's initial catalog of 20,000 species. The best recent estimates suggest that there are ≈6 million species. More emphasis has been placed on counts of free-living species than on parasitic species. We rectify this by quantifying the numbers and proportion of parasitic species. We estimate that there are between 75,000 and 300,000 helminth species parasitizing the vertebrates. We have no credible way of estimating how many parasitic protozoa, fungi, bacteria, and viruses exist. We estimate that between 3% and 5% of parasitic helminths are threatened with extinction in the next 50 to 100 years. Because patterns of parasite diversity do not clearly map onto patterns of host diversity, we can make very little prediction about geographical patterns of threat to parasites. If the threats reflect those experienced by avian hosts, then we expect climate change to be a major threat to the relatively small proportion of parasite diversity that lives in the polar and temperate regions, whereas habitat destruction will be the major threat to tropi-

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cal parasite diversity. Recent studies of food webs suggest that ≈75% of the links in food webs involve a parasitic species; these links are vital for regulation of host abundance and potentially for reducing the impact of toxic pollutants. This implies that parasite extinctions may have unforeseen costs that impact the health and abundance of a large number of free-living species.

The year 2008 marks the tercentenary of the birth of Linnaeus, the scientist who first provided a formal classification for biological diversity. In the initial edition of *Systema Naturae* (Linnaeus, 1735), Linnaeus included a group of species—the *Paradoxa*—that confounded his classification or whose actual existence he questioned. Pelicans, for example, were placed in *Paradoxa* because Linnaeus thought they might reflect the over-fervent imaginations of New World explorers. Parasitic worms were also placed in *Paradoxa* because Linnaeus initially thought that they might be confused, or misplaced, earthworms. In later editions of *Systema Naturae*, Linnaeus revised his opinions about both pelicans and parasitic worms. We now know much about parasites but still rarely think of them as major components of biodiversity. One primary goal of this chapter is to revise this misconception and quantify the ubiquity of parasitism as a lifestyle. We then attempt to quantify how many parasite species are threatened with extinction.

To quantify the abundance and potential loss rates of parasite biodiversity, we initially need to quantify these measures for their host species. For this we have briefly synthesized the work of May (1988, 1990a), Stork (1993), Purvis and Hector (2000), and Erwin (2004). We then restrict our tally of parasite diversity to parasitic helminths of the vertebrates: trematodes, cestodes, acanthocephalans, and the parasitic nematodes. This tally will synthesize and update an excellent book-length treatment of this question by Poulin and Morand (2000, 2004). Although our approach uses the best available data for the most comprehensively studied groups of parasites and hosts, our attempts to quantify species numbers and extinction rates for parasites still provide underestimates of the true global values of these parameters for several taxonomic and pragmatic reasons: vertebrates are a small component of host diversity, vertebrates are parasitized by a subset of the helminths, and helminths are not the most fully described parasite taxa.

HOW MANY SPECIES ARE THERE ON EARTH?

Beginning in 1988, Robert May (1988, 1990a, 1992) cogently argued that our inability to estimate the diversity of species on Earth provided a sad and somewhat self-centered testimony to human inquisitiveness.

After collating data on the numbers of species in each major taxon, May (1988) concluded that our knowledge of vertebrates far exceeded that of invertebrates and protists. The principal reason for the deficient quantitative assessment of diversity in invertebrates and protists was the limited number of trained taxonomists (especially in the tropics, where most of the world's biodiversity resides). Although strides have been made to build capacity in these areas over the last 20 years (Janzen, 1994; Smith and Rogo, 2005), the number of taxonomists working in the museums of most tropical countries today is roughly comparable to the number that worked in Sweden's museums 250 years ago (in Linnaeus's time, at the dawn of taxonomy). Consequently, classifying and naming species continues to proceed at a slow and uneven rate.

Erwin's (1982) work on beetles in tropical forest canopies provided a dramatic illustration of our lack of comprehension of how many extant species exist. Erwin's initial estimates suggested there might be as many as 30 million species of beetles in the world's tropical forests [considerably more than the 20,000 species initially estimated by John Ray (1627–1705) and cataloged by Linnaeus in *Systema Naturae* (Linnaeus, 1735)]. Erwin's estimate of global insect diversity stimulated a series of articles that used a variety of different approaches to estimate total species numbers. Erwin (2004) recently reviewed this literature, and his summary table is illustrated in Fig. 4.1. Two key patterns emerge. First, estimates of global spe-

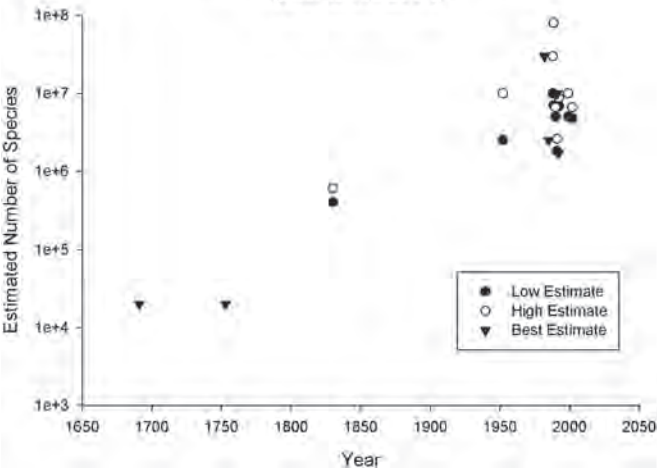

FIGURE 4.1 Estimates since the time of Linnaeus of the number of metazoan species. Data are from Erwin (2004), and the dates for Linnaeus (1735) and John Ray (1691) were estimated from time of publication of their major books on this topic (Erwin, 2004). The most recent sets of estimates sometimes provide a range, or an upper bound, and less frequently a "best estimate" of total species numbers.

cies diversity have increased almost exponentially since Linnaeus's and Ray's original estimates. Second, various numerical estimates of global biodiversity made during the past 20 years concentrate between 3 and 10 million species, of which only 1.4 million have been formally described. It seems unlikely that we will ever achieve a secure estimate of extant species, particularly because many species seem destined for extinction before they are counted, classified, and formally named.

HOW MANY PARASITE SPECIES?

Rohde (1982) provides an additional perspective on the ubiquity of parasitism as a lifestyle by estimating the numbers of parasitic species in each of the major taxa. A graphical representation of these data suggests that ≈40% of known species are parasitic, with parasitism ubiquitous in some taxa and either absent or rare in others (Fig. 4.2).

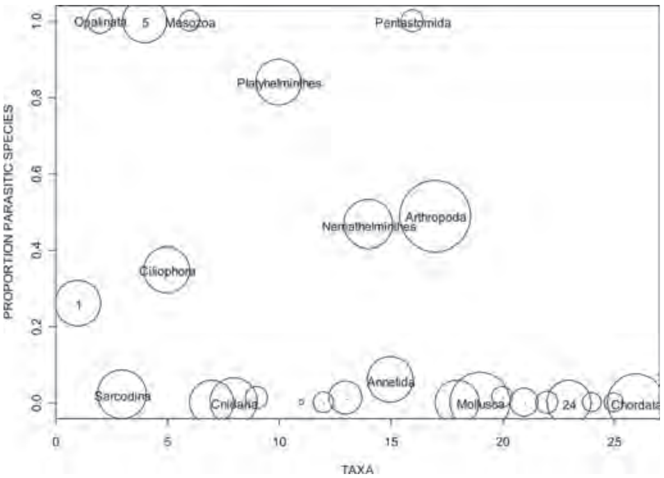

FIGURE 4.2 Relative abundance of different taxa, and the proportion of parasitic species in those taxa [data from Rohde (1982)]. Taxa are numbered along the *x* axis as follows: 1, Mastigophora; 2, Opalinata; 3, Sarcodina; 4, Apicomplexa/Microspora; 5, Ciliophora; 6, Mesozoa; 7, Porifera; 8, Cnidaria; 9, Ctenophora; 10, Platyhelminthes; 11, Priapulida; 12, Entoprocta; 13, Nemertina; 14, Nemathelminthes; 15, Annelida; 16, Pentastomida; 17, Arthropoda; 18, Tentaculata; 19, Mollusca; 20, Echiurida; 21, Sipunculida; 22, Hemichordata; 23, Echinodermata; 24, Pogonophora; 25, Chaetognatha; 26, Chordata. The area of a circle corresponds to the natural log of the total number of species in a taxon, and the center of the circle corresponds to the proportion of parasitic species in that taxon.

Poulin and Morand (2000, 2004) have used several approaches to further examine the potential diversity of parasitic helminths. They point out that many of the problems that beset estimates of free-living biodiversity also confound estimates of parasite diversity. In particular, the rate of discovery of new parasite species has grown linearly or exponentially in some well-studied helminth taxa. In contrast, sampling of parasite diversity from the most diverse parts of the world is thin at best. For example, Cribb *et al.* (2002) estimated that in groupers (Epinephelinae)—one of the largest and most common groups of marine fish—parasitic trematodes have been recorded from only 62 of the 159 species, and from only 9 of 15 genera. The absences reflect a paucity of sampling; most species were examined at only one location. Moreover, not only are most host species unstudied, but no tropical species of grouper has been exhaustively sampled for trematodes. This creates a significant problem for estimating global species richness of parasites based on extrapolations from known patterns of host specificity.

While acknowledging these problems, Poulin and Morand (2000, 2004) extrapolated estimates of specificity from studies of parasites in the relatively well-surveyed vertebrates. Their summary table suggests that there are at least 50% more parasitic helminth species (≈75,000) than there are vertebrate hosts (45,000) (Table 4.1). [The number of parasite species could actually be much higher, especially because fish species are hugely undersampled (Cribb *et al.*, 2002; Hoberg and Klassen, 2002), as are the reptiles, amphibians, and indeed all vertebrate groups in the tropics (Brooks and Hoberg, 2000).]

Modern molecular methods have revealed a further bias that suggests that we have underestimated parasite species richness. These methods have revealed significant numbers of "cryptic species" of parasite that look morphologically similar but are sufficiently genetically distinct so as to represent different species [e.g., see Hung *et al.* (1999); Jousson *et al.* (2000); Haukisalmi *et al.* (2004); Perrot-Minnot (2004)]. The number of cryptic parasite species previously classified as a single morphologically recognized species can sometimes be disconcertingly high [for example, Miura *et al.* (2005) distinguished eight genetic species for a single morphospecies]. The issue of cryptic species will significantly distort estimates of global parasite species richness based on extrapolations from host specificity and mean numbers of parasites observed per host species. One of the basic elements of Poulin and Morand's extrapolation is the number of hosts used by a parasite (Table 4.1). As parasites use more hosts, estimates of global diversity go down. However, many studies have found that cryptic species parasitize only a subset of the species originally recognized as hosting a parasite morphospecies [e.g., see Reversat *et al.* (1989) and Jousson *et al.* (2000)]. Thus, considerations of cryptic species might well

TABLE 4.1 Estimates of Mean Number of Parasite Species per Host, Mean Host Specificity, and Global Species Richness for the Parasitic Trematodes, Cestodes, Nematodes, and Acanthocephalans That Parasitize Each of the Major Vertebrate Taxa of Hosts [after Poulin and Morand, 2004)]

	Host Species (known no. of host species)						
Parasite Species	Chondrichthys (843)	Osteichthys (18,150)	Amphibia (4,975)	Reptilia (6,300)	Aves (9,040)	Mammalia (4,637)	Total (43,945)
Mean parasite species per host species							
Trematoda	0.12	2.04	1.27	1.06	3.24	1.61	
Cestoda	2.71	1.57	0.27	0.39	3.67	1.89	
Acanthocephala	—	1.01	0.19	0.42	0.72	0.28	
Nematoda	0.48	1.49	2.82	2.15	3.32	3.90	
Mean host specificity							
Trematoda	2.00	6.35	5.40	1.77	2.97	2.01	
Cestoda	1.69	6.38	4.75	2.21	2.36	1.89	
Acanthocephala	—	14.95	6.74	12.50	8.35	4.32	
Nematoda	2.67	10.28	5.27	2.12	3.28	6.07	
Estimated global species richness							
Trematoda	51	5,831	1,170	3,773	9,862	3,714	24,401
Cestoda	1,352	4,466	283	1,112	14,058	4,637	25,908
Acanthocephala	—	1,226	140	212	779	301	2,658
Nematoda	152	2,631	2,662	6,389	9,150	2,979	23,963
Total	1,555	14,154	4,225	11,486	33,849	11,631	76,930

lead to a further doubling of the estimates of global parasite richness, suggesting that there could be >300,000 parasitic helminth species using vertebrates as hosts.

HOW MANY PARASITE SPECIES PER HOST SPECIES?

In the best-studied taxa, an average mammalian host species appears to harbor two cestodes, two trematodes, and four nematodes, and an acanthocephalan is found in every fourth mammalian species examined. Each bird species harbors on average three cestodes, two trematodes, three nematodes, and one acanthocephalan (Poulin, 1999; Poulin and Morand, 2000, 2004). None of these estimates take possible unrecognized cryptic species into account, but, in general, helminths that parasitize avian species seem to be less host-specific than those that parasitize mammals. Ultimately, the parasitic fauna of any host species reflects its interaction with the host's feeding niche, latitudinal range, and social system.

The survey of parasite diversity provided by Poulin and Morand raises many unanswered questions. Do host species from monospecific genera harbor more specialized parasites than do species from more diverse genera or families? What is the status of parasite diversity in the tropics? Nearly all parasite data for nonhuman hosts have been collected from the commonest species of the temperate zone.

Studies of helminth parasites of fishes suggest that latitudinal gradients of diversity are more complex than are those of their hosts. There are many more fish species in the tropics, so we might initially expect there to be more parasite species as well. But, if high host diversity in the tropics leads to low densities of each host species, then some host-specific parasites might be unable to maintain viable populations in their low-density tropical hosts, in which case host-specific parasites and their hosts could exhibit reverse gradients of species diversity. Empirically, the two best studied parasite taxa show opposite trends: tropical fish species have more monogenean parasites per host species than do those in temperate zones (Rohde, 1982, 1999, 2002), whereas tropical fish species have less diverse gut parasites than do their temperate counterparts (Choudary and Dick, 2000; Poulin, 2001). The monogeneans predominantly live on the skin and gills of fish and are either transmitted directly by physical contact between hosts (in the case of the Gyrodactyloidea, the most speciose monogenean group) or via short-lived infectious stages known as oncomiracidia. Thus, monogeneans may be more host-specific, assuming that transmission occurs primarily between individuals living in conspecific social groups. In contrast, the gut parasites may tend to be host-generalists because they characteristically enter a host via predation on infected prey species that may be a component of the diet of many host species. More research is needed to understand how these differences in habitat and transmission mode drive the different gradients of parasite species diversity.

HOW MANY PARASITES AND WHAT IS THEIR ROLE IN AN ECOLOGICAL FOOD WEB?

An alternative approach to ascertain global estimates of parasite diversity is simply to examine how many parasites are in a specific habitat or ecosystem. We have been undertaking this for salt marshes along the coasts of California and Baja, Mexico (Lafferty *et al.*, 2006a,b; Kuris *et al.*, 2008). The initial results confirm that ≈40% of the species in any location are parasitic on the 60% of species that are free-living. However, consideration of the trophic links of the parasitic species significantly changes our perception of how ecological food webs are structured.

The standard ecological food web is normally considered to be a trophic pyramid, with primary producers on the bottom, fewer species of herbivores on the next level, and even fewer predatory species higher up (Lindeman, 1942). When parasites are included, this pattern is almost literally "turned on its head" (Fig. 4.3); essentially, a second web appears around the free-living web, and this completely changes the level of con-

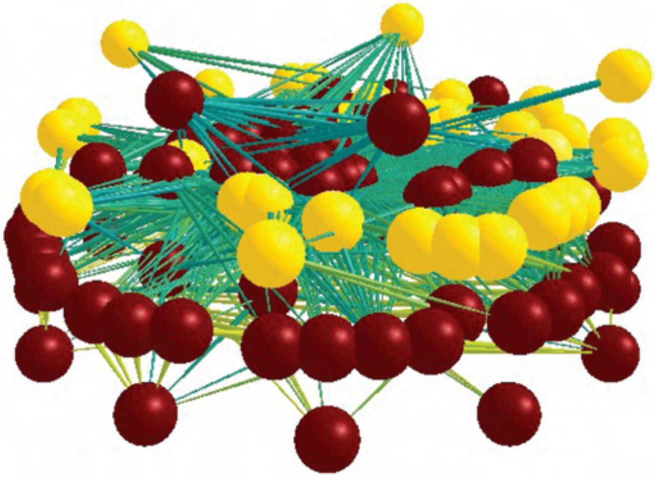

FIGURE 4.3 Three-dimensional visualization of the complexity of a real food web with parasites from the Carpinteria Salt Marsh web using WoW software. Balls are nodes that represent species. Parasites are the light-shaded balls, and free-living species are the dark-shaded balls. Sticks are the links that connect balls through consumption. Basal trophic levels are on the bottom, and upper trophic levels are on the top. Figure from Lafferty *et al.* (2008).

nectivity. The addition of ≈40% more species to the community leads to four times the number of trophic connections between species, thus creating a web that is much more tightly coupled. In many ways, parasite species appear as hidden "dark matter" that holds the structure of the web together, and in ways that are very different from those of free-living species (Fig. 4.3). Furthermore, the web's structure changes from a pyramid to an inverted rhomboid. Predatory species at high trophic levels are now seen to be consumed from within by a diversity of parasites. Animals at lower trophic levels have fewer parasites, but they are often essential hosts for specific stages of parasites that need hosts from two or three different trophic levels to complete the life cycle. When transmitting between trophic levels, only a minority of parasites successfully infect a host; most parasite individuals are consumed as planktonic prey items by many of the species they are trying to parasitize.

Even if a parasite successfully establishes in a host, it is often consumed when the host becomes a prey item in the diet of a predator. Natural selection has made considerable use of this resource–consumer link and allowed parasites to continue their life cycle in the viscera of predatory species. In many cases, the parasites have evolved to modify the behavior of the prey to make it more accessible to the predator, thus significantly increasing transmission efficiency through this stage of the life cycle (Dobson, 1988; Lafferty, 1992). We suspect that the food-web structure observed in salt-marsh communities is common to most natural ecological communities, with parasite species comprising ≈40% of the local species diversity but exerting significant stabilizing forces that hold together the structure of much of the free-living web.

HOW RAPIDLY ARE WE LOSING HOSTS AND PARASITES?

Estimates for the loss of biodiversity use a variety of methods to compare current rates of species extinction against background rates (May *et al.*, 1995; Regan *et al.*, 2001). All of these methods suggest that we are entering a period of mass extinction that is directly comparable to the mass extinctions recorded in the fossil record. Poulin and Morand (2004) used the proportion of threatened hosts in each major vertebrate taxon to estimate the potential threatened number of parasitic species. We have modified their projection to consider different levels of host specificity (Table 4.2). Poulin and Morand's original calculation assumed a direct correspondence between the proportion of parasites threatened and the proportion of hosts threatened. This figure was then adjusted by the degree of host specificity of the parasites. Koh *et al.* (2004) performed a similar analysis, using more sophisticated models on select groups of hosts and parasites for which they acquired good data on host-use patterns. All

TABLE 4.2 Percentage of Vertebrate Species Listed as Threatened by IUCN Red List and the Estimated Numbers of Parasitic Helminth Species That This Puts at Risk of Extinction (upper) [Poulin and Morand (2004), Who Assume That the Proportion of Parasite Species at Risk Equals the Proportion of Hosts at Risk], and Proportion of Parasites at Risk When Corrected for Different Levels of Host Specificity Exhibited by Each Parasite Taxa in Each Host Taxa (lower)

	Host Species (% of host species listed as threatened)						
Parasite Species	Chondrichthys (2)	Osteichthys (2)	Amphibia (2)	Reptilia (3)	Aves (11)	Mammalia (11)	Total
No. of parasite species at risk							
Trematoda	1	117	23	113	1,085	409	1,748
Cestoda	27	89	6	33	1,546	510	2,211
Acanthocephala	—	25	3	6	86	33	153
Nematoda	3	53	53	192	1,007	328	1,636
Trematoda	1	18	4	64	365	203	656
Cestoda	16	14	1	15	655	270	971
Acanthocephala	—	2	0	1	10	8	20
Nematoda	1	5	10	90	307	54	468
Totals (%)	18 (1.13)	39 (0.28)	16 (0.38)	170 (1.48)	1,338 (3.95)	535 (4.60)	2,115 (2.75)

of their data suggest that the relationship between host extinction and parasite species extinction is concave, with parasites (and other dependent species) lost more rapidly than their free-living host species. However, the two groups of parasites that they examined (lice and pinworms of primates) both have very high host specificities, so we would expect quite a tight matching between host extinction and parasite extinction.

The estimates of parasite species extinction rate that Poulin and Morand initially produced failed to account for patterns of host specificity (upper section of Table 4.2) and produced high estimates for loss rates of parasite diversity. When we take host specificity into account, parasitic species seem to go extinct at a lower rate than the host species (lower section of Table 4.2); only ≈3% of helminths (≈2,000 species among 75,000 total) would then seem to be endangered. If our estimates of net parasitic helminth diversity are low by as much as a factor of four, then there could be as many as 10,000 threatened parasitic helminth species. All of this suggests that we are likely to lose considerable numbers of parasitic helminth species before we have had time to obtain specimens that might be identified and classified.

The numbers for parasitic helminth diversity calculated by Poulin and Morand (Table 4.1) suggest that the bulk of parasitic helminth diversity occurs in birds. The majority of these species will have complex life cycles and thus will also depend on host species at lower trophic levels to complete their life cycles. For example, most of the trematode species also require a snail species in which they undergo asexual reproduction, and many will then pass through another intermediate host that will be a prey item in the diet of the bird that acts as the definitive host in which the parasite reproduces sexually. Although the trematode may be able to use a diversity of different bird species as a definitive host, it will most likely be specific to the snail host. As we will show in the next section, projected avian extinctions imply that the spatial patterns of avian loss will be a major driver of the loss of parasite diversity.

WHERE DO AVIAN HOSTS OCCUR?

We have used a nearly complete, geo-referenced database of the geographical distributions of all of the world's 8,750 land-bird species to illustrate the geographic patterns of potential avian host diversity (sea birds and mainly pelagic species are excluded). These data reveal a range of patterns for avian diversity (Fig. 4.4) that are not only fascinating from the perspective of avian evolutionary radiations, but also raise an intriguing set of questions about patterns of parasite geographical diversity.

For example, avian species diversity peaks in the tropics and declines rapidly toward the poles. Broadly similar patterns occur at higher taxo-

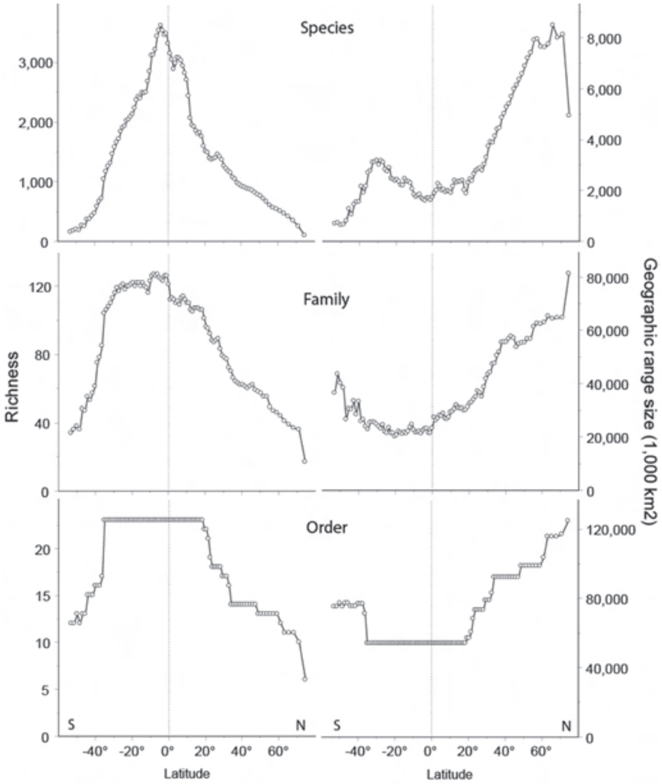

FIGURE 4.4 Latitudinal relationship between taxonomic richness (*left*) and geographical range size (*right*) for all 9,754 bird species at three different taxonomic levels: species, family, and order. Only breeding distributions were included, and range sizes were measured over dry land and averaged across all species, families, or orders occurring at a given latitudinal band.

nomic levels, but the rates of latitudinal decline are less rapid, because many of the bird orders and families that evolved in the tropics have representatives that radiated into the temperate and arctic zones. In contrast, few evolutionary radiations in the temperate (or arctic) zones have spread back into the tropics. A major future challenge is to examine how the pattern of parasitic helminth diversity maps onto this pattern of host diversity. Our null expectation is that the two patterns should be concordant, but the high levels of host species diversity per order (and per family) in the tropics would suggest we are likely to see more generalist parasites (using closely related host species) in the tropics and more specialist species in the taxonomically poorer temperate and arctic zones.

However, studies from Beringia (in the high Arctic) suggest that significant levels of parasite interchange occur during intermittent periods of climatic warming when host species from the arctic regions of different continents disperse across the poles and provide new host opportunities for their parasites (Hoberg and Adams, 1992).

If the range size of avian species, orders, and families increases with distance from the equator (Fig. 4.4), might we see a similar effect with the range size of parasites? If so, then this will have caused us to further underestimate the diversity of parasites in the tropics, because the area sampled by tropical parasite taxonomists is tiny. Similarly, do the nested patterns of geographical diversity for the hosts reflect pulses of radiation and speciation between the tropics and temperate zones after past periods of climate change, and would we see similar radiations of diversity if we traced the phylogenies and geographical distributions of avian parasites at different taxonomic levels? Surveys suggest that the diversity of human parasites is significantly higher in the tropics (Low, 1990; Guernier *et al.*, 2004), but as we saw above, this is less clearly the case for fish parasites. If similar latitudinal patterns occur in avian orders and genera, and if parasites are responsible for driving significant components of sexual selection that lead to host speciation, then we might expect complex patterns of geographical variation in parasite diversity at the taxonomic level of host order and family. Unfortunately, the parasite data with which to test these hypotheses are unavailable.

LOSS OF AVIAN DIVERSITY: CLIMATE CHANGE VERSUS HABITAT LOSS

We have used the geographic distribution database for birds described above to evaluate potential impacts of projected environmental change on each of the major continents (Jetz *et al.*, 2007). The Millennium Ecosystem Assessment (MEA) used four quantitative scenarios to examine how land cover would change across the land surface of the Earth over the next 50 and 100 years (Alcamo *et al.*, 2005; Carpenter *et al.*, 2005). The scenarios were driven by quantitative climate models derived from the Intergovernmental Panel on Climate Change (IPCC) and projections of human population growth, wealth, and other socioeconomic parameters across regions (Image_Team, 2001). In these projections, rates of land conversion would be driven either by climate change or by the need for new agriculture land. The four MEA scenarios were defined by whether or not governments take a proactive or reactive response to environmental management, and by whether the world's nations become more unified and interactive or they become more protectionist and isolated (Cork *et al.*, 2005). Jetz *et al.* (2007) used the output from the scenarios to examine the potential impact on the world's land-bird species under the simplifying assumption of stationary geographic ranges.

Projections of land-use change based on the different MEA scenarios have revealed consistent geographical patterns of impact. The projections differ mainly in the magnitude of their impacts, with the reactive and isolationist scenarios experiencing about twice the rate of habitat conversion as the scenarios for proactive and connected worlds (Carpenter *et al.*, 2005). In all cases, the impacts of climate change in the next 50 to 100 years are largest in polar regions. Although climate change also has effects in the temperate and tropical zones, these are almost completely masked by human agricultural expansion, particularly in the tropics. This pattern of land-use change will interact directly with the geographical variation in the range sizes of bird species. In particular, bird species with small ranges are at a much greater risk of extinction than those with large geographical ranges (Jetz *et al.*, 2007). Unfortunately, most avian species living in the tropics have small ranges and a significant number will experience large declines in range size due to agricultural habitat conversion. In contrast, the minority of species that live in the polar zones are projected to experience large potential loss of range due to climate change, but they usually have sufficiently large geographical ranges that some of their environment remains habitable (Fig. 4.5) (Jetz *et al.*, 2007).

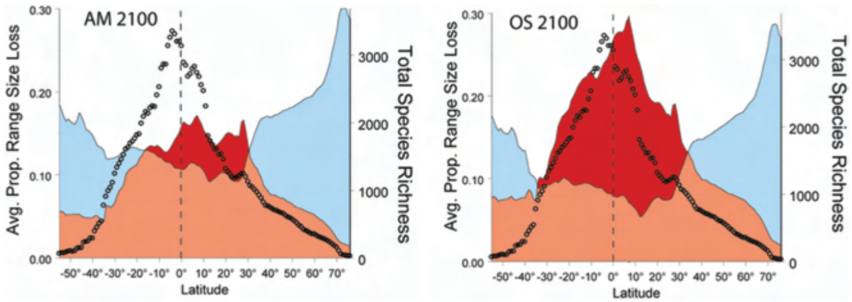

FIGURE 4.5 The relationship between geographic range size and percentage range transformations for all of the world's 8,750 land birds under two MEA scenarios of future land-use change. (*Left*) "Adaptive mosaic" (which assumes a world with open political dialogue that deals proactively with environmental problems). (*Right*) "Order from strength" scenario (which assumes a more insular political world that only deals retroactively with environmental problems). Jetz *et al.* (2007) provide complete detail for how the analyses were developed. The dots illustrate number of avian species, lightest shading denotes range change due to climate change, and black illustrates land-use change due to agricultural expansion.

HOW MANY BIRD PARASITES HAVE WE LOST?

Parasite species ultimately depend on their host species for persistence (Stork and Lyal, 1993; Koh *et al.*, 2004). The analysis of future bird extinctions described above suggests that rare and specific tropical parasite species will be lost rather rapidly as tropical bird species decline in range and abundance, or go extinct. However, common parasite species that can use a range of host species in the temperate zone may be significantly buffered against extinction (Bush and Kennedy, 1994; Brooks and Hoberg, 2007). This suggests that the relationship between loss of host species and loss of parasite species will tend to be concave (Koh *et al.*, 2004). At best, the relationship between host extinction rate and parasite extinction rate may be sigmoidal in shape, with the point of inflexion determined by the relative proportion of species that are specific to individual host species. Unfortunately, insufficient data exist to accurately examine the shape of these relationships. In general, we expect that inefficiently transmitted parasites (or pathogens) will tend to be lost first, whereas efficiently transmitted species with low host specificity (due to their use of vectors or trophic transmission) will persist at low host densities.

Although a parasite species that can use a range of host species will not go extinct if one of its hosts species declines to extinction, it is likely that the abundance and geographical range of a parasite species will decline as each potential host species is lost or itself declines in range and abundance. This suggests that parasitic species will tend to decline at a faster rate than their hosts. Furthermore, as noted by Poulin and Morand (2004) and Koh *et al.* (2004), parasites with complex life cycles that require multiple host species will be more prone to extinction as natural habitats are destroyed or disrupted than will be pathogens with direct life cycles. Additionally, given the existence of minimum thresholds of host density below which many parasites cannot sustain recruitment (Anderson and May, 1986), many parasites will go extinct even before their hosts disappear. Arguably the least endangered parasites will be sexually transmitted pathogens and pathogens transmitted from infected females to their offspring (Kuris *et al.*, 1980; Smith and Dobson, 1992). Although highly host-specific, such pathogens can persist in smaller host populations than the normal directly transmitted pathogens (Smith and Dobson, 1992; Altizer *et al.*, 2003).

ECOSYSTEMS SERVICES LOST?

It may be that the loss of a significant proportion of the world's parasitic helminth species is a tragedy only for parasitologists. Indeed, once a host species loses its parasite species, it might experience an increase in population size that could prevent it from declining to extinction. However, this perspective ignores several important "ecosystem services" that parasites perform. For example, parasites often act as regulators of host abundance, which in the case of generalist pathogens may lead to strong frequency-dependent control over relative host abundance throughout the host community (Dobson, 2004). Another example involves parasitic helminths that may play a major role in buffering levels of pollution in natural communities (Sures, 2003).

REGULATION OF HOST POPULATIONS AND RELATIVE ABUNDANCE IN COMMUNITIES

Parasites create a diversity of links in food webs that at first sight may appear atypical, but they are not unusual in nature—more than 75% of links in natural food webs probably involve parasites (Lafferty *et al.*, 2006b). Because many parasites use multiple competing hosts on the same trophic level, their population dynamics may be modeled by sets of coupled differential equations that take the general form

$$ds_i / dt = b_i(S_i + I_i) - d_i S_i - \beta_{ij} S_i \sum_{j=1}^{n} I$$

$$dI_i / dt = \beta_{ij} S_i \sum_{j=1}^{n} I_j - (d_i + \alpha_i) I_i$$

where we assume that each host species *i* has species-specific birth and death rates (*b* and *d*) and experiences transmission of the pathogen at a rate β_{ij} from infected individuals of species *j*. Infection converts each susceptible host, *S*, into an infectious individual, *I*, that experiences an increased pathogen-induced mortality rate, α. When compared with single-species infectious disease models, the presence of interspecific transmission is usually strongly stabilizing for a wide range of interspecies transmission rates that are less than the rates of within-species transmission (Dobson, 2004). However, when rates of interspecific transmission approach rates of within-species transmission, the pathogen acts as a powerful mechanism of indirect competition [as a shared natural enemy (Holt and Lawton, 1994)] that can drive some host species extinct.

We can examine the potential consequences of this for more complex systems by recasting the differential equation models within the matrix framework that describes the initial trajectory of a perturbation to the whole food web. Thus, each element of the matrix represents a pairwise interaction between each pair of species in the food web (Pimm, 1982; Pascual and Dunne, 2005). If we retain our classification of each host as susceptible and infected, then the parasite in effect enters the food web as two species. Both have the phenotype of the host (although the feeding preferences might change after infection). However, the infected hosts now effectively have the genotype of the pathogen, and transmission acts as a birth process converting susceptible hosts into infected individuals that can also be considered as "shared natural enemies" of uninfected hosts of all susceptible species. We can briefly examine a submatrix of food web interactions for specialist and generalized pathogens within a food web.

Specialist parasites and competing host species

$$\begin{array}{c|cccc}
 & \mathrm{A} & \mathrm{Ia} & \mathrm{B} & \mathrm{Ib} \\
\hline
\mathrm{A} & - & - & - & 0 \\
\mathrm{Ia} & + & 0 & 0 & 0 \\
\mathrm{B} & - & 0 & - & - \\
\mathrm{Ib} & 0 & 0 & + & 0
\end{array}$$

Pathogens shared between competing host species

$$\begin{array}{c|cccc}
 & \mathrm{A} & \mathrm{Ia} & \mathrm{B} & \mathrm{Ib} \\
\hline
\mathrm{A} & - & - & - & - \\
\mathrm{Ia} & + & 0 & + & 0 \\
\mathrm{B} & - & - & - & - \\
\mathrm{Ib} & + & 0 & + & 0
\end{array}$$

In these two matrices of species interaction, host species A and B compete with each other for resources such as food or space, and each host species has a pathogen associated with it (thus infected hosts of species A are characterized as "species" Ia). In the case of specialist parasites (upper matrix), infected hosts of species A cannot infect species B; the complementary case operates for the lower matrix, where both species of pathogen infect both species of host. The main consequence of host species sharing nonspecific parasite species is that several elements of the interactions matrix have to be converted (across the main diagonal) from "zeros" into "plus–minus" consumer–resource relationships. If we are concerned with the stability properties of the web, then May (1973) has shown that the dominant eigenvalues of this matrix have to be negative if there is to be any hope of web stability. In May's initial formulation, increased species diversity and hence increased connectance should reduce the probability that the web is stable. However, although the net effect of shared pathogens is to increase the connectance of the food web, this occurs in a subtle and important way. Namely, the conversion of specific pathogens to generalized pathogens greatly increases the proportion of "across-diagonal" plus–minus links in the web. Because the product of their interaction is always negative, adding more summed negative terms increases the chances that this eigenvalue will be negative (Allesina and Pascual, 2008). More specifically, adding shared pathogens to the food web significantly increases the proportion of negative cross-product terms relative to positive product terms produced by competition (where negative times negative = positive!). This effect generalizes: As we increase the species diversity of the web, destabilizing competitive interactions will increase at a maximum rate of $(n^2 - n)/2$, whereas potentially stabilizing shared pathogen interactions increase at the significantly faster maximum rate of n^2.

Similar effects arise when we consider parasites with complex multiple host life cycles. These infectious agents confound traditional concepts of food-web structure because they feed on several different trophic levels within different host species during the course of their life cycle. They also act as food resources to species on different trophic levels as they pass through their free-living stages. Usually, <1% of the energy-rich, free-living infective stages of a parasite ever manage to infect a host; the other 99% are eaten by planktivorous species. Parasites with this type of life cycle can again be incorporated into food-web models. Initial results with matrix models of the form described above suggest that such parasites will also have key stabilizing effects on the structure of food webs because they also add pairwise sequences of "plus–minus" resource–consumer interactions at every stage of their life cycle, and these will consistently increase the probability that the dominant eigenvalues of the linearized system will be negative. Furthermore, generalist parasites with complex multihost life cycles also introduce long circular loops of relatively weak links into the web; theoretical analysis by Neutel *et al.* (2002) suggests that these may also be important in imparting stability to food webs.

Thus, generalist parasites and those with complex life cycles potentially play important roles in regulating the relative abundance of their free-living host species. Whereas generalist species with direct transmission are likely to be buffered from extinction by the rescue effect of at least one host remaining abundant, parasites with complex life cycles will depend highly on the host species in the life cycle to which they are most specifically adapted. The trematode and acanthocephalan species that are recorded as adult worms from scores of vertebrate host species often depend entirely on a single species of mollusk or amphipod that serves as their intermediate host. Thus, snails or other invertebrates that invade natural ecosystems and replace crucial host species within the complex life cycles of parasites may lead to losses of parasite diversity that cascade throughout the food web.

REGULATION OF CONCENTRATION OF POLLUTANTS

Recent work by Sures (2003, 2004) and colleagues has shown that parasitic helminths may play a substantial role in concentrating and ultimately removing heavy metals and other pollutants from their hosts. They can concentrate and withstand levels of cadmium, zinc, and other heavy metals that are up to 2,000% above background levels (and ≈1,000 times greater than the levels sustained by snails and other host species widely used as monitors of toxicants and pollutants). Parasites achieve this level of concentration through their preference for absorbing bile from the guts of their hosts. Most vertebrates attempt to minimize the impact of harmful substances in their gut by surrounding the offensive items with bile and passing them out in their feces. However, significant amounts of the substance are reabsorbed with bile in the lower intestine. This occurs to a much lesser extent in hosts parasitized by parasitic helminths; many of these parasites selectively absorb bile as a food source, thereby removing the pollutants from the host's gut and concentrating them in the worm (Sures, 2003).

Results from studies of salt-marsh ecosystems suggest that metazoan parasites constitute up to ≈3% of the biomass of major animal groups in the system (Kuris *et al.*, 2008). If parasites are 3% of the animal biomass, then their ability to superconcentrate pollutants may mean that they contain 30–50% of the mass of pollutants in the system. This would amount to a formidable ecosystem service! We note, however, that this assumes that the many different groups of metazoan parasites studied in Kuris *et al.* (2008) are as efficient at absorbing pollutants as the adult stages of helminths in the guts of vertebrates studied by Sures (2003, 2004). Nevertheless, a relatively small biomass of adult worms in vertebrates may sequester a significant proportion of the pollutants that would otherwise disrupt the viability of host populations. This suggests that if parasites are lost via extinction of their hosts, or via replacement of intermediate hosts by nonviable invasive host species, then the free-living host species may experience enhanced levels of pollutants. Parasitic helminths of humans supply a similar ecosystem service when they selectively remove both pollutants and allergens from human guts. This provides a viable explanation for why allergies are much more common in human societies that have successfully reduced their parasite loads than in those that still bear a significant burden of parasitic helminths (Yazdanbakhsh, 2002).

In conclusion, we suggest that there is reason to join Sprent (1992) and Windsor (1995) in mourning the loss of the parasitic species that disappear when their hosts go extinct (Stork and Lyal, 1993; Koh *et al.*, 2004). If significant increases in extinction rates now apply to birds, mammals, amphibians, and fish, then it is almost inevitable that extinction rates in host-specific parasite species are increasing at least concomitantly. As we develop a deeper understanding of food-web structure and dynamics, it seems increasingly likely that parasitic helminths play a major role in ecosystem function and may even supply important economic services to humans. Understanding the structure of food webs remains among the deepest scientific challenges of the 21st century. Parasites will play a key role in developing this understanding, yet they are at least as threatened by mass extinction as are many other species—potentially even more so. A healthy functioning ecosystem will have a full complement of parasitic species (Hudson *et al.*, 2006). Fully determining the role that parasites play in regulating natural systems remains a major challenge for ecologists and evolutionary biologists. If the major job of conservation biologists is to maintain fully functional food webs, then it is crucial that we consider parasites as a vital and necessary component of biodiversity. It is then but a small step to acknowledge that these animals are well worth conserving.

ACKNOWLEDGMENTS

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Part II

CONTEMPORARY PATTERNS AND PROCESSES IN PLANTS AND MICROBES

Charismatic animals are most often the focus of conservation efforts, but much of the biological world is potentially at extinction risk from current human activities. Chapters in this section address some potential concerns about biodiversity and extinction in plants and microbes.

The anthropogenic introduction of alien species is perhaps second only to habitat loss as a cause of recent and ongoing species extinctions. The problem is especially acute on oceanic islands, where countless native animals have gone extinct following the arrival of humans and their hitchhiking associates. In Chapter 5, Dov Sax and Steven Gaines examine historical records from islands around the world to ask whether native plant species likewise often have gone extinct when exotic plants were introduced and became naturalized. The answer seems to be a clear no, at least yet. One possibility is that native plant species on islands are accumulating an extinction debt that will be paid in future species losses; alternatively, the number of native plus exotic plants on islands may reach a stable equilibrium or saturation point that is much higher than the endemics alone had been able to achieve. The authors examine the evidence pertaining to these competing hypotheses, and explore the ramifications for future plant biodiversity on islands depending on which scenario proves to be more nearly correct.

The task of tallying extant species and estimating extinction risks can be daunting even for relatively well-studied biotas. Such scientific exercises can also be highly informative, as Stephen Hubbell and colleagues illustrate in Chapter 6 by applying neutral biodiversity theory (Hubbell,

2001) to estimate the number, abundance, range size, and extinction risk (under alternative scenarios of future habitat loss) for medium- and large-sized trees in the Amazon Basin. Their quantitative analysis suggests that more than 11,000 tree species inhabit this extraordinarily biodiverse region. The good news for biodiversity conservation is that more than 3,000 of these species have large population sizes and therefore are likely to persist well into the future (barring catastrophic climatic or other environmental changes). The bad news is that for the large class of rare Amazonian trees (more than 5,000 species likely to consist of fewer than 10,000 individuals each), estimated near-term extinction rates are 37% and 50%, respectively, under optimistic and non-optimistic projections concerning ongoing deforestation practices by humans.

With regard to tallying numbers of taxa and characterizing local, regional, or global patterns of biodiversity, microbes offer even stiffer challenges than many plant and animal taxa. In Chapter 7, Jessica Bryant and colleagues associated with Jessica Green tackle such problems on a meso-geographic scale by applying DNA sequence data (from the 16S ribosomal gene) and other information to questions about microbial biodiversity along an elevational habitat gradient in the Colorado Rocky Mountains. Bacterial taxon richness along their climatic-zone transect decreases monotonically from lower to higher altitudes, and detectable phylogenetic structure (non-random spatial clustering of related taxa) occurs at all elevations. In comparable analyses of plants along the same gradient, the authors uncovered qualitatively different outcomes with regard to both taxon richness and species assemblage. These findings indicate that whatever ecological and evolutionary forces shape microbial communities, the biodiversity patterns will not always mirror those in macrobiota.

An important follow-up issue for microbial (or other) taxa is whether the composition of natural communities predictably influences the responses of those communities to environmental alteration. Traditionally, microbial communities often have been treated as “black boxes” in functional ecological models, a situation that Steve Allison and Jennifer Martiny would like to see rectified. In Chapter 8, these authors review experiments and observations from the scientific literature to address questions about the composition of a microbial community following exposure to environmental perturbations. Is the microbial community resistant to the disturbance (tend not to change in taxonomic composition)? Is it resilient (change in makeup but then return quickly to the pre-disturbance condition)? If an altered composition is sustained, is the new community functionally redundant to the original? Based on the authors’ literature review, the answers to these questions usually seem to be “no,” “no,” and “no.” Allison and Martiny emphasize that all such conclusions remain provisional pending further research of this nature, and they suggest several promising empirical and conceptual approaches.

5

Species Invasions and Extinction: The Future of Native Biodiversity on Islands

DOV F. SAX* and STEVEN D. GAINES[†‡]

Predation by exotic species has caused the extinction of many native animal species on islands, whereas competition from exotic plants has caused few native plant extinctions. Exotic plant addition to islands is highly nonrandom, with an almost perfect 1 to 1 match between the number of naturalized and native plant species on oceanic islands. Here, we evaluate several alternative implications of these findings. Does the consistency of increase in plant richness across islands imply that a saturation point in species richness has been reached? If not, should we expect total plant richness to continue to increase as new species are added? Finally, is the rarity of native plant extinctions to date a misleading measure of the impact of past invasions, one that hides an extinction debt that will be paid in the future? By analyzing historical records, we show that the number of naturalized plant species has increased linearly over time on many individual islands. Further, the mean ratio of naturalized to native plant species across islands has changed steadily for nearly two centuries. These patterns suggest that many more species will become naturalized on islands in the future. We also discuss how dynamics of invasion bear upon alternative saturation scenarios and the implications these scenarios have for the future

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retention or extinction of native plant species. Finally, we identify invasion-motivated research gaps (propagule pressure, time-lags to extinction, abundance shifts, and loss of area) that can aid in forecasting extinction and in developing a more comprehensive theory of species extinctions.

Species invasions have contributed to the extinction of many species worldwide (Clavero and Garcia-Berthou, 2005), particularly on islands (Sax *et al.*, 2002; Steadman, 2006). These extinctions have occurred disproportionately among taxonomic groups. For example, birds have lost many species, both in absolute terms and relative to their total number of species, whereas plants have lost few species (James, 1995; Sax *et al.*, 2002; Blackburn *et al.*, 2004). The lack of recorded extinctions in plants does not appear to be due to a lack of knowledge, particularly on well-studied islands like New Zealand, where both historic and fossil records suggest that few native plant species have been lost (Sax *et al.*, 2002). Why so few plant species have been lost is somewhat of a mystery, particularly considering the thousands of exotic plant species that have been introduced to islands (Sax *et al.*, 2002). This near-lack of plant extinctions to date raises the obvious question of whether this trend will continue. In particular, should we expect few additional plant species to go extinct—even on individual islands where hundreds or thousands of exotic plant species have invaded? Should ongoing and future invasions eventually lead to mass extinction events among island plant taxa?

Our ability to accurately forecast future extinction events is limited by shortcomings in current ecological and evolutionary theory. In particular, we have a relatively poor understanding of the processes that ultimately limit how many species can inhabit any given place or area. One important concept, however, that arises from several prominent theories of species diversity is that for any given set of environmental conditions there is a "saturation point" that bounds the number of species a place or region can support (MacArthur and Wilson, 1963, 1967; Hubbell, 2001; Tilman, 2004). There are two basic ways that a saturation point for species richness could operate. First, the total number of species present in an area could be maintained as a balance between extinction and colonization. At the saturation point, the addition of new colonizing species results in the local extinction of a like number of previously established species. We refer to this as "extinction-based saturation," which is consistent with Island Biogeography Theory (IBT) (MacArthur and Wilson, 1963, 1967). Second, the total number of species in a place could be maintained by suppression of colonization. A saturation point is reached if the invasion of new species is inhibited by species already present. We refer to this as "colonization-based saturation," which is consistent with the resistance to invasion in niche-based models of species diversity, such as Stochastic Niche Theory (SNT), where the total number of species in a place is determined by how finely resources can be partitioned among species (Tilman, 2004).

These alternative pathways for species saturation have very different implications for the impact of invading species on native plant extinctions. Extinction-based saturation (like IBT) explicitly predicts species turnover, i.e., change in species composition, with the addition of species to islands (MacArthur and Wilson, 1963, 1967). Therefore, once a saturation point has been reached, the continued addition of exotic species should result in the extinction of native species, and the rate of extinction increases as the rate of colonization increases. If this holds true for islands, then we may eventually have dramatic increases in the number of native plant extinctions—particularly if exotics continue to be added in large numbers. In contrast, colonization-based saturation (like SNT) explicitly predicts that the addition of exotic species will become progressively less likely to occur as species richness increases (Stachowicz and Tilman, 2005). Colonization-based saturation (like SNT) also predicts that existing species should benefit from a priority effect that makes them unlikely to be displaced by incoming species—as long as invading species are more or less equivalent to native species in their efficiency in using resources (Stachowicz and Tilman, 2005). If this holds true on islands, then we should expect the rate of naturalization of exotic species to diminish dramatically and few currently established species (both native and exotic) to be at risk of extinction in the future. These are two very distinct views of the future, and distinguishing among these and other alternatives is important. Doing so will help us to advance our basic understanding of ecological and evolutionary theory while simultaneously advancing our understanding of a pressing applied issue, namely the future of plant diversity on islands worldwide.

Here, we evaluate the role of species invasions on the extinction of native species. We begin by examining the International Union for Conservation of Nature database for patterns of extinction in plants and terrestrial vertebrates that have occurred worldwide over the past 500 years. We then focus on patterns of invasion and extinction on islands over the past few hundred years. Next, we consider, with a focus on plants, whether islands are saturated with respect to the total number of species they can support. We also consider what the implications of species saturation are for future plant extinctions. Finally, we explore several research gaps that currently limit our ability to forecast species extinctions.

GENERAL DRIVERS OF EXTINCTION

Humans have caused or contributed to many plant and animal extinctions. Over the past 15,000 years, humans have contributed to extinctions of large fauna on most continents of the world (Barnosky, Chapter 12, this volume). Over the past few thousand years, human colonists and their commensals (such as the Polynesian rat) have contributed to the extinction of thousands of bird species across oceanic islands of the world (Steadman, 2006). Over the past 500 years, humans have reduced the amount of natural habitat worldwide, directly exploited species, introduced exotic species and exotic pathogens, and created many other conditions conducive to species extinction. The total number of recent extinctions is unknown, because many species have likely gone extinct before ever being recorded by science (Wilson, 1992). Estimates of global species loss vary, but based on rates of tropical deforestation and the species–area relationship a fairly typical estimate is 27,000 species lost per year; this is based on a species–area relationship with a z value of 0.15 and an estimate of 10 million species globally (Wilson, 1992). Even with a more conservative estimate of 5 million species on the planet (Primack, 2006), this would still equate to ≈13,500 species lost, or at least committed to extinction, per year. In sharp contrast to such estimates, the number of documented extinctions during the past 500 years is much lower; the International Union for Conservation of Nature, as of November 2007, reports 785 extinctions worldwide. Many other extinctions, not included in this number, have likely occurred, but they have not yet been documented adequately enough to be listed as extinct by the International Union for Conservation of Nature. Consequently, although species listed as extinct by the International Union for Conservation of Nature are likely an underestimate of the total number of extinctions over the past 500 years, those listed provide the most detailed evidence on extinction available.

There has been recent disagreement in the literature about how best to interpret extinction data from the International Union for Conservation of Nature, particularly with regards to the role species invasions play in causing extinctions (Gurevitch and Padilla, 2004; Ricciardi, 2004; Clavero and Garcia-Berthou, 2005). This disagreement has largely been due to the difficulty in ascribing precise causes to species extinctions. The precise mechanisms for any individual extinction are difficult to confidently determine for two reasons. First, extinctions are often caused by multiple factors, such as species invasions, habitat destruction, human exploitation, pollution, and infectious disease (KF Smith *et al.*, 2006). Second, most "documented" extinctions actually involve some speculation about the factors responsible (because few species have been carefully monitored from the point of initial population decline to the point of final extinction). Additionally, it is worth noting that disagreement over species concepts, and disagreement over phylogenetic classifications of individual species, although not an issue for most extinct species, is an important point of debate in some cases. Given these limitations, it seems most appropriate to (*i*) consider whether general trends in the data exist, as opposed to focusing on the details of any one extinction, and (*ii*) focus analyses on those taxonomic groups that have been best studied and documented. Consequently, here we examine general trends in extinction in two of the best studied groups: terrestrial vertebrates and plants.

An analysis of the International Union for Conservation of Nature database on species extinctions reveals several emerging patterns for terrestrial vertebrate and plant species. First, most extinctions have been on islands as opposed to mainlands (Fig. 5.1*A*). This holds true generally when all causes of extinction are pooled (Fig. 5.1*A*) and specifically when only extinctions that exotic species are believed to have contributed to are considered (Fig. 5.1*B*). Second, terrestrial vertebrates have disproportionately gone extinct compared with plants (Fig. 5.1*A*), both in absolute terms and relative to the taxonomic richness of their respective groups. Third, the presumed causes of these extinctions are not evenly distributed among types of species interactions. Predation has been a far more important species interaction in causing extinctions than competition (Fig. 5.1*C*). Indeed, predation alone, i.e., in the absence of other factors like habitat destruction or pollution, is listed as being responsible for the extinction of >30% of vertebrate species (Fig. 1*C*). In contrast, competition is never listed as being the sole factor responsible for species extinction (Fig. 5.1*C*). Further, predation is listed as one of several contributing factors in >40% of terrestrial vertebrate extinctions, whereas competition is listed as a contributing factor in <10% of terrestrial vertebrate extinctions (Fig. 5.1*C*). This means that predation acting alone or in concert with other factors is believed to have contributed to the extinction of close to 80% of all terrestrial vertebrate species, whereas competition has contributed to <10% of these extinctions. This predominance of predation over competition in causing extinctions may be due in part to the broad range of processes that we classify here as "predation," e.g., both human hunting and parasitism (see *Methods*). However, even if we consider predation in the strictest sense to include only carnivorous animal interactions, the qualitative patterns described here are maintained. Further, differences between the role of predation and competition are conserved when considering only those cases where exotic species are believed to have played a contributing role in species extinction (Fig. 5.1*D*); in these cases, the combined influence of predation acting alone and predation acting in concert with other factors is believed to account for 98% of all extinctions. These patterns suggest that terrestrial vertebrates are much more likely to go extinct from predation than competition. This interpretation is consistent with observational and theoretical work by Davis (2003), who suggests that competition should rarely be an important factor in species extinctions. Finally, for plants, we did not evaluate the role of predation versus competition in causing spe-

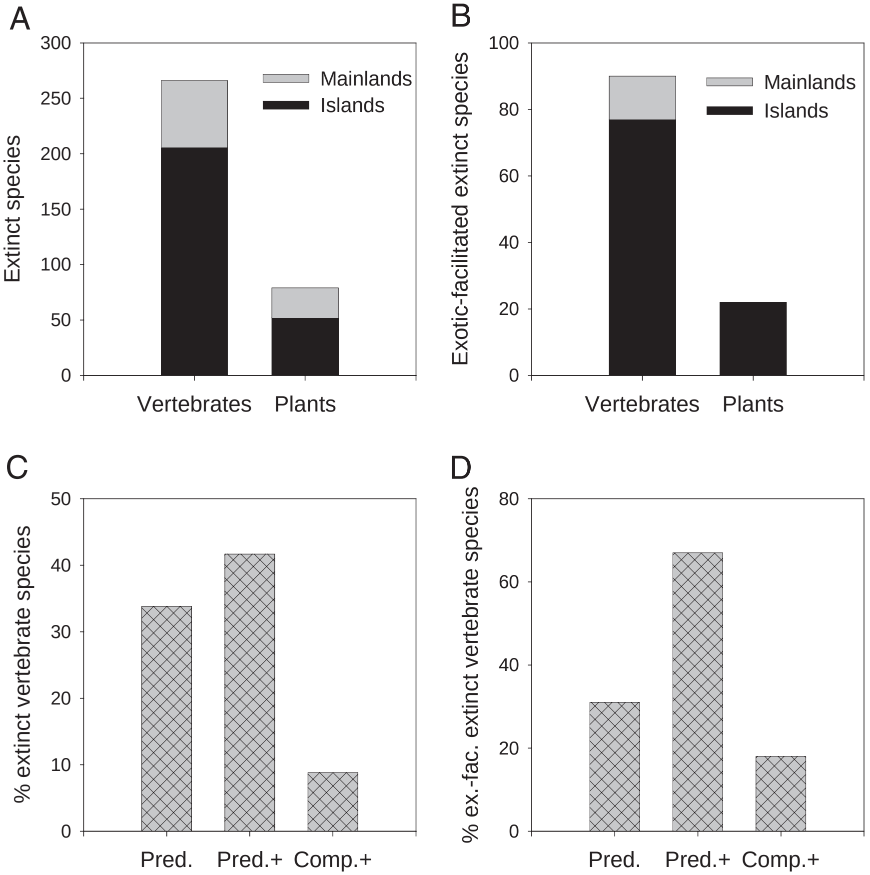

FIGURE 5.1 Extinction patterns over the last 500 years, from the International Union for Conservation of Nature database. (*A*) The majority of documented extinctions have been on islands, as opposed to mainlands, for both terrestrial vertebrates (birds, mammals, reptiles, and amphibians) and plants. (*B*) Extinctions facilitated by exotic species (i.e., in which exotics are listed as at least one of the factors contributing to a species extinction) show the same pattern, with more extinctions on islands, as opposed to mainlands. (*C*) Among the 204 vertebrate species with listed causes of extinction, some form of predation (including human hunting, carnivory, and infectious disease) is cited as the sole factor responsible for species extinctions in 69 (33.8% of) extinctions, predation together with other contributing factors is cited for 85 (41.7% of) extinctions, and competition together with other factors is listed for 18 (8.8% of) extinctions. In no case is competition listed as the sole cause of species extinction. (*D*) Extinctions facilitated by exotic species show similar patterns, with predation listed alone in 31 of 100 extinctions, predation together with other factors listed in 67 extinctions, and competition together with other factors listed in 18 extinctions.

cies extinctions because the degree of certainty generally associated with listed causes of plant extinctions in the International Union for Conservation of Nature database seemed too speculative. Still, if predation is the true cause of most species interaction-based extinctions then perhaps this can help to explain why competition from invasive plants has led to so few plant extinctions—at least so far.

INVASIONS AND EXTINCTIONS ON ISLANDS

Patterns of species invasions and extinctions have been well documented across a wide variety of islands and for a number of taxonomic groups (Chown *et al.*, 1998; Sax *et al.*, 2002; Sax and Gaines, 2003; Blackburn *et al.*, 2004). In general, many species of plants, vertebrates, and invertebrates have been introduced to islands (Eldredge and Miller, 1995; Chown *et al.*, 1998; Sax *et al.*, 2002). Many of these introduced species have become naturalized, i.e., they have formed self-supporting populations capable of perpetuating themselves. Islands have also lost many native species; among vertebrates, extinctions have been greatest for bird species, largely because most other vertebrate groups are relatively depauperate on islands (Lomolino *et al.*, 2006). In contrast to birds, plants have generally suffered few extinctions on islands (James, 1995; Sax *et al.*, 2002). For example, in New Zealand, 38 of 91 native land bird species have become extinct, whereas only 3 of >2,000 native plant species have become extinct (Sax *et al.*, 2002). Overall, these patterns of extinction and naturalization have led to large changes in net species richness on islands around the world. Bird richness on most oceanic islands has remained largely unchanged, because the number of extinctions has been largely matched by the number of exotic birds that have become naturalized (Sax *et al.*, 2002). This relative consistency in net bird richness may be important in understanding and predicting future extinctions, but is not a "good" thing from a conservation perspective, because it means that many unique endemic species have been lost and replaced by more cosmopolitan species from mainlands (McKinney and Lockwood, 1999). In contrast to birds, mammal richness has increased dramatically, particularly on oceanic islands, which have few native mammal species (Blackburn *et al.*, 2004). Freshwater fish richness has also increased, because few native fishes have gone extinct (at least so far), whereas many exotic species have become naturalized (Sax and Gaines, 2003). Invertebrate richness may also have increased, because many invertebrates have become naturalized on islands, e.g., >2,500 species on Hawaii alone (Eldredge and Miller, 1995), but records of extinction are less certain, so it is difficult to know how net richness has changed without additional investigation. Finally, vascular plants have seen dramatic increases in richness across both continental and oceanic islands, because many exotics have become naturalized, whereas few native species have gone extinct (Sax and Gaines, 2006).

Increases in plant richness show several distinct patterns. First, comparisons between mainlands and islands and among island types (land-bridge versus oceanic) show repeatable quantitative differences; mainland areas have increased in plant species richness least, land-bridge islands have increased more, and oceanic islands have increased the most. For example, counties in California have increased on average by 17%, the California Channel Islands have increased by 44%, and oceanic islands have increased by 104% in richness (Sax and Gaines, 2006). Second, increases in richness on some islands have been sufficiently large that these isolated systems now approximate the richness of continental areas. For example, the addition of naturalized plants to Hawaii has pushed its net plant richness up to levels typical for an area of equal size in mainland Mexico (Sax and Gaines, 2006). Third, the average increase in richness observed across oceanic islands is highly regular, with most islands showing a strikingly consistent doubling in net plant richness (Sax *et al.*, 2002).

The doubling in plant richness on oceanic islands is due to a tightly correlated one-to-one relationship between native and naturalized plant species, with 96% of the variation in naturalized plant richness explained solely by native plant richness (Fig. 5.2). Other island characteristics indi-

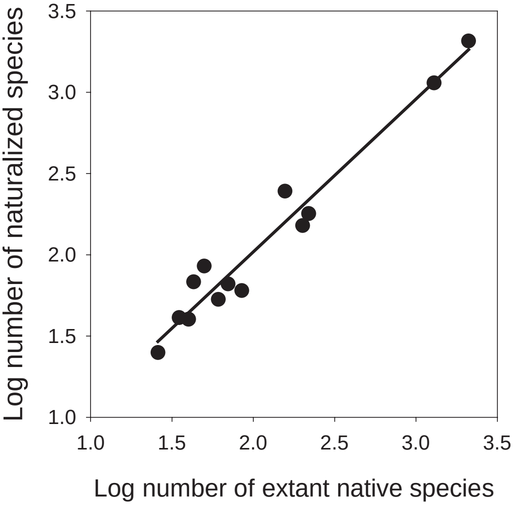

FIGURE 5.2 Native and naturalized plant richness are highly correlated across oceanic islands. The log number of extant native plant species explains 96% of the variation in the log number of naturalized plant species. See Appendix Table 5A.1 for a list of islands and richness values.

vidually explain far less variation in the richness of naturalized species. For example, human population size (79%), island area (71%), island maximum elevation (49%), and date of European settlement (31%) explain significant amounts of the variation but account for far less than that of native species richness. Indeed, even a multiple regression analysis with these and other island characteristics generates a model that accounts for less of the variation in naturalized species richness than is explained by native richness alone (see *Methods*). It is unclear why native plant richness is such a good predictor of naturalized plant richness, but the strength of the relationship suggests that it may provide clues into understanding how richness patterns are likely to change in the future.

Plant invasion patterns provide several lines of evidence that suggest islands might be "filling-up" or becoming "saturated" with species. First, the most species-poor islands (oceanic as opposed to continental) have increased in plant richness the most. Second, many islands are now coming close to matching the species richness levels of continental environments. Third, patterns of increase are highly consistent among oceanic islands, where a close to perfect doubling in species richness of plants has occurred. This doubling might represent a new saturation point for species richness. If this has occurred and a saturation point has been reached, then it would be valuable to know the mechanism by which it has done so, e.g., whether it arose from colonization-based or extinction-based saturation. Alternatively, it would be valuable to know whether no saturation point has been reached. Distinguishing among these alternatives is critical, because they paint very different pictures for the future for plant biodiversity on islands.

EVALUATING COLONIZATION-BASED SATURATION

Colonization-based saturation will occur if the probability of adding new species to an area decreases over time as net richness increases—at some point, as an area fills up, the probability of adding any additional species will become so low that an effective saturation point will be reached (Stachowicz and Tilman, 2005). In some ways, this is a special case of Elton's invasion hypothesis (Elton, 1958), which postulated that species-rich regions would be more difficult to invade than species-poor ones. In regards to islands, if a colonization-based saturation point has been reached, then new species cannot be added unless existing species are removed. This situation appears to have occurred for birds on islands, where native birds that were driven extinct (largely by naturalized mammal predation and human hunting) have been replaced by an approximately similar number of naturalized bird species [most of which invaded after the natives were already extinct (Sax *et al.*, 2002)]. The importance of colonization-based saturation for birds is further corroborated by patterns of invasion in Hawaii, where birds introduced earlier were more likely to become established and persist than those introduced later, when naturalized richness was higher (Gamarra *et al.*, 2007). For groups like plants, which have had few extinctions and many introductions, islands were presumably not saturated by colonization-based mechanisms before species introductions. If, however, oceanic islands have now reached a colonization-based saturation point for plants, then the probability of introduced plant species becoming naturalized on islands should have decreased over the past 200 years as more and more of these species became naturalized. One way this could manifest is as an asymptote in the cumulative number of exotic plant species that became naturalized over time.

We evaluate the possibility that plants have reached a colonization-based saturation point on oceanic islands by examining time series of exotic species additions to individual islands through time (see *Methods*). A complete list of analyzed islands and their naturalized richness values through time are described in the Appendix. Our results show no evidence of an asymptote in number of plant species that have become naturalized through time on any of the islands analyzed, which we illustrate with patterns of naturalization on six individual islands (Fig. 5.3). Instead, the number of naturalized plant species has increased in an approximately linear manner over time, with some potential evidence for exponential increases in a few cases (Fig. 5.3). Also in a few cases, and most notably for Heron Island, there appears to be a slight leveling-off in the number of naturalized species for the very last date recorded; this leveling-off is due to a procedural artifact in how naturalizations are tallied. Because exotic species that are recorded for the first time are typically not classified as being naturalized (because there is no evidence yet that they have established self-perpetuating populations), the total number of naturalized species will generally be underestimated in the last time step (see *Methods*).

In addition to change within individual islands, we also analyzed patterns of change across islands. To do this, we constructed 20-year bins as points of comparison through time (see *Methods*). Currently, the average ratio across islands of naturalized-to-native plant species is ≈1:1. Our results show that this ratio has changed fairly steadily through time, from 1860 to 2000, with no evidence for an asymptote in the rate of change (Table 5.1). Only the final time step shows a leveling-off, but this is due to a procedural artifact (see *Methods*). A second way to illustrate change across islands is with comparisons of regressions through time between the log number of native and naturalized species. To do this, we used the same 20-year bins. Our results show that the slope of these log-log relationships has been fairly consistent through time, which we illustrate with all of the statistically significant regression lines for 20-year bins (Fig. 5.4*A*). Nonsig-

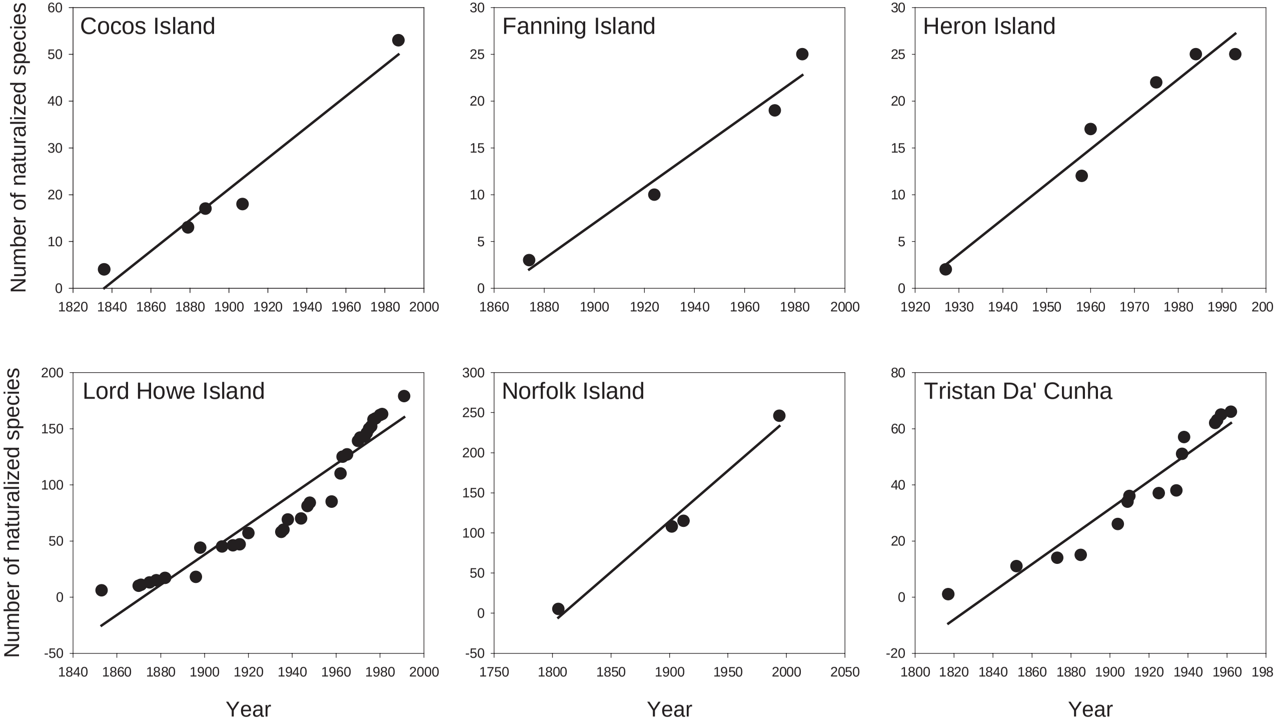

FIGURE 5.3 Naturalized plant richness has increased on oceanic islands in an approximately linear fashion over the past 200 years. Regression lines are all highly significant. None of these islands show evidence of an asymptote in cumulative richness of naturalized species over time.

TABLE 5.1 Ratio (and Standard Error) of Naturalized to Native Plant Species on Oceanic Islands

Year	Ratio	SE
2000	1.07	0.11
1980	1.07	0.14
1960	0.70	0.13
1940	0.52	0.15
1920	0.44	0.09
1900	0.31	0.09
1880	0.15	0.03
1860	0.07	0.04

nificant regression lines for 1860, 1940, and 1960 occurred in periods when relatively few historical surveys were conducted on these islands such that few data points are available for analysis (see Appendix text). The regressions from 2000 and 1880, when a relatively large number of individual data points are available, illustrate the consistency in slope among these periods (Fig. 5.4*B*). The consistency in the slope but change in intercept implies that the proportion of naturalized-to-native species has generally been consistent across islands within any given time interval but different

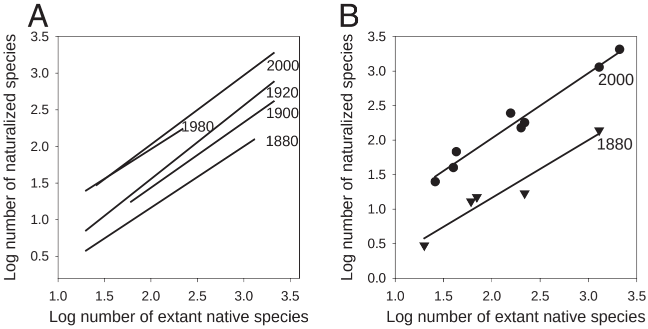

FIGURE 5.4 Across 20-year time intervals from 1880 to the present, the slope of log-log regressions between native and naturalized richness has been relatively constant, whereas the intercepts have changed; this implies that the 1:1 relationship currently observed between native and naturalized richness is a recent phenomenon but that, at repeated points during the past 120 years, there has been a consistent ratio of native-to-naturalized species across islands. (*A*) Regression lines are illustrated for each 20-year interval that had a significant relationship; limited data reduced the statistical power for the 1860, 1940, and 1960 time intervals. (*B*) The regression lines and individual data points are shown for the two time intervals with the greatest amount of data.

among time intervals. This suggests two things. First, it suggests that there is something uniform about the relationship between native and naturalized species across these islands. Second, it suggests that the particular 1:1 relationship observed today is transient. At the current rate of change, the average ratio between naturalized-to-native species on oceanic islands should be ≈3:2 by the year 2060.

There is no evidence of a decrease in the rate of exotic addition of plants to individual islands or across islands over the past 200 years. This suggests that more plant species will continue to be added to these islands in the future. On first consideration, this could be interpreted as strong evidence against the operation of colonization-based saturation for plant species on these islands. However, because the rate of exotic propagule pressure, i.e., the total number of exotic species being introduced per unit time, is unknown, we cannot assess whether the probability of colonization is declining. It is conceivable, and perhaps not unlikely, that propagule pressure of exotic species has been increasing exponentially. If this were true, then the observed linear increase in the total number of naturalized plant species would actually signal a declining probability of naturalization through time—which would be consistent with colonization-based saturation. Therefore, data on rates of propagule pressure over time are needed to fully evaluate the importance of colonization-based saturation for plants.

EVALUATING EXTINCTION-BASED SATURATION

Extinction-based saturation occurs when the per species extinction rate on the island increases to match the rate of new colonizations. Unlike colonization-based saturation, where an island at saturation will experience little change in species composition, extinction-based saturation necessarily involves species turnover. To date, native plants show no evidence of extinction-based saturation on islands, because thousands of exotic plant species have become naturalized, whereas relatively few native species have been lost (Sax *et al.*, 2002). Likewise, previously established naturalized species also appear not to be pushed out by the establishment of additional naturalized plant species. For example, on Lord Howe Island, only 4 of 183 species that have become naturalized have been lost through time. So, with an important caveat, neither natives nor already established exotic species show evidence to support extinction-based saturation.

The caveat to the conclusion that extinction-based saturation is not prevalent in plants is tied to the time course of extinctions. There is enormous uncertainty in how long extinctions may take to manifest. It is conceivable that extinctions already set in motion by existing alterations of island biotas could take hundreds or thousands of years to come to completion. Such time lags to extinction could create a large "extinction debt" (Tilman *et al.*, 1994) that will be paid in the future even without future exotic introductions. Therefore, as with colonization-based extinction hypotheses, we cannot fully evaluate whether extinction-based saturation is in operation. There is little evidence to suggest that species richness of plants on islands is saturating at this time, but this conclusion may need to be revised in the future.

FUTURE OF PLANT DIVERSITY ON ISLANDS

The composition of plant species on islands has been in a rapid state of flux during the past two centuries, because thousands of exotic plant species have been added to island floras. Despite efforts in some regions to control new introductions, we expect that still more exotic plant species will be added to islands over the next century. Even if colonization-based saturation is occurring and the probability of establishment is decreasing, ample introductions may have already occurred to compensate for a declining probability of naturalization. In fact, we see little evidence to support the conclusion that the flow of propagules to islands will be reduced in the near future. Many countries, such as the United States, currently lack or fail to enforce regulations ample to prevent many invasions from occurring (Lodge *et al.*, 2006). Even in those cases where rigorous importation laws exist and are enforced, as in New Zealand, there will generally be a large "bank" of potentially invading species that are already present. For example, in New Zealand, >22,000 exotic plant species that have not yet become naturalized are grown in the country (Duncan and Williams, 2002). Many of these plants have the potential to escape cultivation and become naturalized components of the flora (Sullivan *et al.*, 2005; Williams and Cameron, 2006). Further, global warming and changing environmental conditions many promote the establishment of many species that previously were unlikely to establish naturalized populations. The total number of plant species already present (but not yet naturalized) on most islands around the world has not been tallied, but the numbers are likely to be substantial [e.g., the estimate for Hawaii is ≈8,000 plant species (Eldredge and Miller, 1995)]. Given the substantial size of these species banks and the likely continued import of additional species, it seems likely that most islands will continue to see the addition of exotic species to their naturalized floras in the future.

The ultimate consequence of these exotic species additions for native diversity is still difficult to determine with certainty. We see three primary alternatives with respect to exotic plant invasions and their impact on native species. First, saturation may be unimportant for plant species or, at least, not important at or near the levels of diversity currently present

TABLE 5.2 Alternative Forecasts of Exotic Naturalizations and Native Extinctions of Plant Species on Islands

Scenario	Naturalizations	Extinctions
No saturation	Many	Few
Colonization-based saturation	Few	Few
Extinction-based saturation	Many	Many

on islands. If this is true, then we might expect many more exotic species to be added without consequent extinctions of native plant species (Table 5.2). Second, if colonization-based saturation points are being approached, then we might expect rapid declines in the rate at which exotic species become naturalized in the future; importantly, we would also then expect few of the native plant species on these islands to go extinct (Table 5.2). Third, if extinction-based saturation points are being approached or have been exceeded but are masked by long times to extinction, then we would expect newly introduced exotics to continue to become naturalized and many native species to be on a pathway to extinction (Table 5.2). In each case, we predict an increase in naturalized plant richness but with different magnitudes and vastly different outcomes for native species extinctions. Unfortunately, on the basis of current data, we cannot distinguish among these dramatically different views of future change in island biotas. Fortunately, there are key types of data that could be acquired and key theoretical questions that could be explored that can help to distinguish among these alternatives. Such insight is critical to advancing ecological theory and informing our understanding of how best to use a limited number of conservation resources in preserving the unique biota of islands worldwide.

GAPS IN EXTINCTION RESEARCH

We believe that there are four research gaps that must be addressed to improve our understanding of the consequences of species invasions for the future of native biodiversity. First, propagule pressure of exotic species must be better understood. To date, propagule pressure has been poorly studied in nearly all ecosystems. Some important attention has been paid to records of bird introductions (Cassey *et al.*, 2004), but few other groups have received the same attention (Lockwood *et al.*, 2005). In part, this is due to the difficulty of reconstructing records for groups where introductions have not been well documented. Nevertheless, for plants, a careful historical survey of seed catalogs and import records could undoubtedly provide critical insight on rates of introductions. Second, time lags for species extinction must be better studied. Time lags to extinction have received very limited attention. Some important work was done by Diamond (1972), and a smattering of more recent papers exist (Brooks *et al.*, 1999), but here too the bulk of attention has been on birds. A greater effort is needed to understand dynamics of time lags to extinction, particularly how these may vary across taxonomic groups and geographic areas. Third, we need to more carefully consider and examine how exotic invasions change the abundance patterns of native species. Although abundance for most native species is expected to decline after invasions, the patterns of these declines may be very important in predicting whether extinctions are likely in the future. In particular, it is important to know which species pay the largest cost; the long-term consequences will differ greatly if most of the abundance declines in native species are borne by those species that were previously most abundant, as opposed to those species that were already naturally rare. Fourth, we need to understand how the transformation of large areas into exotic-dominated ecosystems influences extinction of native species through reduction in total available habitat. The species–area relationship is currently one of the most actively used tools for predicting species loss (Gurevitch and Padilla, 2004), yet its application to exotic-dominated habitat loss has been poorly studied. It is unclear whether the species–area relationship can be used in such circumstances to predict future species loss and, if so, then how accurate such predictions are likely to be. The answer is likely to depend on the extent to which patterns of area loss are congruent with species distributions (Seabloom *et al.*, 2002) and on the degree to which natives are excluded from exotic-dominated habitats. Collectively, these gaps in our knowledge create large uncertainty in forecasts of the future responses of island biotas to species introductions. Certainly, there is a pressing need for new data and insights if we cannot distinguish among the polar extremes of (*i*) there is little risk to native plant species on islands from future exotic introductions and (*ii*) a large fraction of native plant species on islands are already on a path to extinction. Hopefully, future work on the interplay between species invasions and extinctions can more fully resolve these issues and, in the process, help us to develop a more comprehensive theory of species extinctions.

METHODS

International Union for Conservation of Nature Extinction Analysis

Accounts of all 785 species listed as "extinct" were downloaded from the International Union for Conservation of Nature database (www.iucnredlist.org) in November 2007. Those species comprising the terrestrial vertebrate groups (birds, mammals, reptiles, and amphibians; 258 species) and plants (87 species) were considered further. Species accounts were used to classify each species as being from a mainland or an island. Only species restricted to islands were listed as "island" species. Included in these tallies are three marine mammals, which we listed as "mainland" for the purposes of these analyses. Species accounts were also used to tally the factors listed as having contributed to species extinction. To do so, both the annotated list of contributing factors, and the text description were examined for each species. We classified extinction factors into three categories: predation, competition, and other factors. Predation includes pairwise species interactions that are positive for one species and negative for the other; this included any of the following: human hunting (including any form of direct human exploitation of a species), carnivorous predation, herbivorous predation, parasitism, and infectious disease. "Competition" included interactions where species competed for resources. All other factors, such as habitat loss and pollution, were considered to be "other factors." Tallies were compiled for species listed as (*i*) only being impacted by predation, (*ii*) impacted by predation together with other factors, and (*iii*) impacted by competition together with other factors. In no case was competition listed as the sole factor causing a species extinction. These same tallies were repeated for the subset of extinct species listed as having been impacted by an "alien," i.e., nonnative or exotic, species.

Island Characteristics

Island characteristics are recorded in Appendix Table 5A.1. Prehistoric occupancy, date of European settlement (for uninhabited islands) or first date of trade with Europeans (for islands already inhabited), latitude, island elevation, island area, human population size, and island occupation history are taken from references described in Sax *et al.* (2002) and as cited in Appendix Table 5A.1. Native and naturalized richness were tallied from the literature after applying a standardized set of criteria to published work. These criteria defined native and naturalized plant species as those believed to have self-supporting populations, such that species believed to be ephemeral were not included. Further, species that are "cryptogenic," i.e., possibly native or exotic, were excluded from these tallies. See Sax *et al.* (2002) for a complete discussion of these criteria and their application. Native and naturalized richness recorded in Appendix Table 5A.1 reflect the most up-to-date values available; these values differ slightly from those recorded in Sax *et al.* (2002), particularly where a more detailed accounting of historical records has provided additional information on species status.

Multiple Regression Analysis

A multiple regression analysis was performed to explain variation in the log number of naturalized plant species on islands. Predictor variables included history of occupation, time of European settlement/trade, latitude, log of island elevation, log of island area, and log of human population size (Table 5A.1). Several variables (as indicated above) were log-transformed to meet the assumption of normally distributed data. Stepwise analyses were performed by using the backward and forward procedures for adding and removing variables. The probability for a variable to enter the model was set at 0.250, and the probability for a variable to leave was set at 0.100. The best model constructed (judged by lowest AIC value and statistically significant predictor variables) has three predictors: history of occupation, log of elevation, and log of human population size; the model has an adjusted R^2 value of 0.91. All statistical analyses were performed in JMP software, Version 5.0.1.

Historical Data on Naturalized Plants

Data were compiled from the literature, using the criteria described above in *Island Characteristics*. Because sampling efforts varied among historic accounts of the flora, the number of exotics recorded in the Appendix are "range-through" data—such that species believed to be established at two points in time are recorded here as being established at all points of time between these. Therefore, if a survey in the 1800s and the modern flora both list a plant as established, then it was assumed to occur on the dates between these, even if it was not recorded on one of the interim dates. In most cases, this resulted in relatively minor alterations from the number of species recorded at any one point in time. This standardization allowed islands where only range-through data were available to be compared with those where all counts were independent. This procedure is particularly appropriate for large, topographically complex islands where individual species are easily missed on any one survey of an island. The one island considered here where this procedure may not have been necessary is Heron Island—a small (19-ha) island in the Great Barrier Reef. However, the differences on Heron Island between range-through and point-time data are relatively small, as indicated in the Appendix. Range-through data were not calculated for New Zealand; consequently, data from 1940 (when a range-through calculation is anticipated to make a substantial difference in recorded values) were not used in analyses of change in naturalized richness through time (see Appendix). Note that range-through and point-time data are always equivalent for the first and last time steps of any given island. The most recent (modern) publications used as data sources for islands are listed in Sax *et al.* (2002); older records used to reconstruct the historical data are cited within these modern publications.

Analyzing Change in Naturalized Richness

Data on change in naturalized richness through time (Appendix) were analyzed in multiple ways. First, data were plotted on individual islands over time (Fig. 5.3). Second, the mean ratio of naturalized to native richness was calculated in 20-year intervals over the past 140 years (Table 5.1); e.g., the penultimate interval, 1980, extended from 1971 to 1990. Native richness was held constant across these ratio analyses, using the currently recorded values (Appendix Table 5A.1); this was done because the actual number of native species on islands has changed very little over the past 140 years, because few species have been lost and presumably few native species gained during this time period. Naturalized richness values were taken from the Appendix. When more than one date was available from a single 20-year time interval, then the date closest to the midpoint of the time period was used; if two dates were equally close to the midpoint, then the one closest to dates analyzed for other islands in that time period was used. Third, these same native and naturalized values were plotted by 20-year time intervals (Fig. 5.4).

Note that the last date recorded for any individual island is subject to a procedural artifact that reduces the total number of naturalized species. This artifact lowers the number of naturalized species not just for individual islands, but also for mean estimates of naturalized species across islands. This procedural artifact occurs because exotic species are only counted as "naturalized" if they are seen (*i*) in multiple places on an island within a single time step or (*ii*) within the same area across multiple time steps, i.e., across two or more survey periods that are separated sufficiently for at least one turnover in generation time to have occurred [see Sax *et al.* (2002) for a full discussion]. Consequently, species seen in only one place on an island and recorded from only the most recent island survey will not be considered to be naturalized unless they persist to the next survey period, when the number of naturalized species from the previous time period would then be revised upward.

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APPENDIX: NATURALIZED VASCULAR PLANT SPECIES ON ISLANDS OVER TIME

Years listed below refer to the most recent survey or plant collection date and not to the date of publication of a manuscript, even though, in many cases, the collection and publication date are the same. Following each year, the number of naturalized species is indicated in parentheses. See *Methods* in the main text for a brief description of criteria used in tallying the number of naturalized species and Sax *et al.* (2002) for a thorough discussion of these criteria and data sources.

Christmas Island (Indian Ocean). 1898 (14), 1904 (21), 1993 (151).

Cocos (Keeling) Islands. 1836 (4), 1879 (13), 1888 (17), 1907 (18), 1987 (53).

Easter Island. 1911 (17), 1917 (31), 1991 (68).

Hawaiian Islands. 1886 (139), 2002 (1140). These values are taken directly from the literature.

Heron Island. Range-through data: 1927 (2), 1958 (12), 1960 (17), 1975 (22), 1984 (25), 1993 (25). Uncorrected data: 1927 (2), 1958 (12), 1960 (16), 1975 (22), 1984 (24), 1993 (25). Given Heron Island's small size, range-through corrections are likely to overestimate the number of plants present in any single time step. For consistency of comparison among islands, range-through data were used in our analyses, but the differences here between methods are relatively minor.

Lord Howe Island. 1853 (6), 1870 (10), 1871 (11), 1875 (13), 1878 (15), 1882 (17), 1896 (18), 1898 (44), 1908 (45), 1913 (46), 1916 (47), 1920 (57), 1935 (58), 1936 (60), 1938 (69), 1944 (70), 1947 (81), 1948 (84), 1958 (85), 1962 (110), 1963 (125), 1965 (127), 1970 (139), 1971 (142), 1973 (143), 1974 (146), 1975 (150), 1976 (152), 1977 (158), 1978 (159), 1980 (162), 1981 (163), 1991 (179).

Mangareva Island. This island was not used in analyses of change in naturalized plants through time, because the date of most recent plant collections could not be determined.

Nauru Island. 1933 (22), 1981 (84), 1988 (85).

New Zealand Islands. 1853 (61), 1867 (169), 1906 (528), 1925 (576), 1940 (593), 1999 (2065). The large size and topographic complexity of New Zealand (relative to other islands) creates greater uncertainty about whether particular exotics are naturalized or not in individual time steps. Consequently, data values were taken directly from the literature and range-through values have not been calculated (see *Methods* in the main text). Data from 1940 were excluded from our analyses because there is a large set of species that may or may not have been naturalized at that time, but data from the other time steps were used. Note that some additional dates are available for a subset of the vascular plants (the non-monocots), but these data were not used here, as our analyses were focused on vascular plants.

Norfolk Island. 1805 (5), 1902 (108), 1912 (115), 1994 (246).

Pitcairn Island. 1991 (40).

Tabuaeran (Fanning) Island in the Northern Line Islands. 1874 (3), 1924 (10), 1972 (19), 1983 (25). The Northern Line Islands, as a set of four islands (Table 5A.1), were used for Fig. 5.2 and the multiple regression analyses. Tabuaeran Island, which has a more complete temporal record, was used for analyses of change through time: Table 5.1, Figs. 5.3 and 5.4.

Tristan da Cunha Island. 1817 (1), 1852 (11), 1873 (14), 1885 (15), 1904 (26), 1909 (34), 1910 (36), 1925 (37), 1934 (38), 1937 (51), 1938 (57), 1954 (62), 1955 (63), 1957 (65), 1962 (66).

TABLE 5A.1 Island Characteristics

Island or Archipelago	Naturalized Plant Species	Native Plant Species	Occupation History[a]	European Settlement[b]	Latitude[c]	Elevation, m	Area, km^2	Human Population[d]
Christmas	151	201	Uninhabited	1888	–10.8	357	135	3,214
Cocos (Keeling)	53	61	Uninhabited	1826	–12	9	14	300
Easter	68	43	Inhabited	1864	–27.2	511	173	2,300
Hawaii[e]	1,140	1,292	Inhabited	1778	22.4	4,169	16,636.5	1,321,000[f]
Heron	25	26	Uninhabited	1923	–23.4	4	0.19	132[g]
Lord Howe	179	219	Uninhabited	1834	–31.8	875	14.6	371
Mangareva	60	85	Inhabited	1834	–23.2	441	13	860
Nauru	85	50	Inhabited	1835	–0.7	70	20.7	10,605
New Zealand[h]	2,065	2,104	Inhabited	1795	–40.9	3,764	268,670	3,662,265
Northern Line Island[i]	41	35	Inhabited	1854	3.9	5	368.7	2,155
Norfolk	246	157	Inhabited	1788	–29	318	36.8	1,905
Pitcairn	40	40	Inhabited	1790	–25.8	347	4.2	66
Tristan da Cunha	66	70	Uninhabited	1810	–37.2	2,060	103.2	296

[a] More detailed accounts of occupation history at the time of European contact are available in Sax *et al.* (2002).

[b] Date of first European settlement for uninhabited islands or first European trade for inhabited islands.

[c] The negative sign indicates degrees South latitude. Values are taken from standard data sources, except for Hawaii, New Zealand, and the Northern Line Islands; their latitudes are calculated as the midpoint between their northern- and southern-most points (as indicated in notes *e,h, i*).

[d] Values are from the UNEP Island database (http://islands.unep.ch/), from the CIA world fact book, and from the literature. Population estimates were matched as closely as possible to the year in which the last plant survey of an island was conducted (Appendix text). Note that on some islands, e.g., Christmas Island, that population size has decreased in recent years.

[e] Hawaii includes all islands in the chain from Hawaii to Laysan.

[f] The population size for Hawaii includes permanent residents as well as an estimate of annual visitors.

[g] Heron Island's effective population size is estimated as the number of visitor days from a typical year in the 1980s (48,000 visitor days) divided by the number of days in the year. See Sax *et al.* (2002) for data source.

[h] New Zealand includes North, South, and Stewart Islands, as well as near-shore islands associated with these three islands.

[i] Northern Line Islands include Kiritimati, Tabuaeran, Teraina, and Palmyra.

6

How Many Tree Species Are There in the Amazon and How Many of Them Will Go Extinct?

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New roads, agricultural projects, logging, and mining are claiming an ever greater area of once-pristine Amazonian forest. The Millennium Ecosystem Assessment (MA) forecasts the extinction of a large fraction of Amazonian tree species based on projected loss of forest cover over the next several decades. How accurate are these estimates of extinction rates? We use neutral theory to estimate the number, relative abundance, and range size of tree species in the Amazon metacommunity and estimate likely tree-species extinctions under published optimistic and nonoptimistic Amazon scenarios. We estimate that the Brazilian portion of the Amazon Basin has (or had) 11,210 tree species that reach sizes >10 cm DBH (stem diameter at breast height). Of these, 3,248 species have population sizes >1 million individuals, and, ignoring possible climate-change effects, almost all of these common species persist under both optimistic and nonoptimistic scenarios. At the rare end of the abundance spectrum, however, neutral theory predicts the existence of ≈5,308 species with <10,000 individu-

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als each that are expected to suffer nearly a 50% extinction rate under the nonoptimistic deforestation scenario and an ≈37% loss rate even under the optimistic scenario. Most of these species have small range sizes and are highly vulnerable to local habitat loss. In ensembles of 100 stochastic simulations, we found mean total extinction rates of 20% and 33% of tree species in the Brazilian Amazon under the optimistic and nonoptimistic scenarios, respectively.

> To obtain even a very rough estimate of the total number of species in the [Amazonian] forest community, a hypothesis must be made concerning the relationship between the common and rare species.
>
> Pires *et al.* (1953)

The watershed of the Amazon River and its tributaries is enormous, covering ≈7,179,100 km^2, and the longest dimension of the basin is ≈6,815 km. The Amazon Basin contains ≈40% of the world's remaining tropical forest, much of it still botanically intact, or largely so, particularly in western Amazonia. However, serious concern has been raised about the possibility of large-scale extinctions of tree species in the next several decades, due to the expansion of a network of roads, especially in the Brazilian Amazon (Whitmore and Sauer, 1992; Laurance *et al.*, 2001, 2002; Anonymous, 2006). These roads open undisturbed areas to extractive uses of the Amazon forest in previously inaccessible areas far from rivers and to subsequent clearing of forest for ranching, agricultural crop production, and tree plantations of commercially important species, mostly exotics. Anthropogenic habitat destruction is perhaps the single greatest cause of modern species extinctions (Ehrlich and Ehrlich, 1981; Wilson and Peter, 1988; Wilson, 1989). Climate change may become an even bigger cause of extinction over the next century (Thomas *et al.*, 2004; Williams *et al.*, 2007).

This chapter examines the questions of how many tree species there are in the Amazon and how many of them will go extinct from habitat loss during the next several decades. More than 50 years ago, long before the survival of the Amazon forest became a headline issue, Theodosius Dobzhansky and two experts on the Amazonian tree flora, Pires and Black, made a pioneering attempt to answer the "how many tree species" question from samples of virgin forest in eastern Amazonia in the state of Pará. In their first paper, which reported counts of tree species in several 1-ha plots, they encountered a large fraction of tree species only once (as a single individual) (Black *et al.*, 1950). In their second study (Pires *et al.*, 1953), they increased their plot size to 3.5 ha in the hope that a larger sample size would reduce the number of singleton species, but the problem only got worse rather than better.

Pires and coworkers did not set themselves the ambitious goal of attempting to estimate the number of tree species in all of the Amazon but just in the particular "association" they sampled. Nevertheless, the quote above indicates that Pires *et al.* (1953) were aware of the difficulty of answering the "how many species" question without having a theoretical hypothesis concerning the distribution of relative species abundance. Two primary competing statistical hypotheses were available, then as now: Fisher's logseries (Fisher *et al.*, 1943) and Preston's lognormal (Preston, 1948). The logseries predicts that the most frequent abundance class will be the rarest—singletons, which is what Pires and coworkers observed. Of the 179 species they found, 45 species (25%) occurred just once. Despite this observation, Pires *et al.* (1953) argued that the Preston lognormal was the "most reasonable" hypothesis, although they did not fit or mention Fisher's logseries, of which Preston's paper was a critique. When one does this exercise, Fisher's logseries actually fits their data quite well (Fig. 6.1). But these data were from small plots in forest that was relatively species-poor by Amazonian standards. The question therefore arises: Which of these two distributions is a better fit to the distribution of relative tree species abundance in tropical tree communities in general and, more specifically, to relative tree species abundances in the entirety of the Amazon Basin?

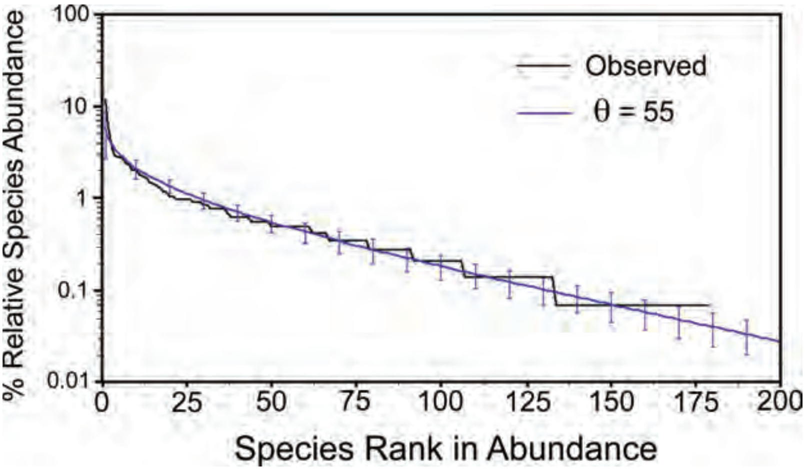

FIGURE 6.1 Fit of Fisher's logseries to the Amazonian relative tree species abundance data of Pires *et al.* (1953).

The answer to this question is highly relevant to the questions posed in the title of this chapter because these two relative-abundance hypotheses yield profoundly different predictions for the total number of tree species in the Amazon as well as for how many of these species are likely to go extinct. The logseries hypothesis predicts a far larger number of species—and that a far larger fraction of these species are rare to very rare—than does the lognormal hypothesis. This is because Preston's (1962) canonical lognormal hypothesis postulates a fixed variance or spread in the distribution of log abundance of species irrespective of sample size. The result of this assumption is that the number of octaves of $\log_2$ abundance separating the commonest and rarest species does not increase with increasing sample size. Consequently, as the abundance of common species increases in larger samples, so the sample abundance of rare species must also increase in logarithmic proportion. The canonical lognormal hypothesis, in turn, implies that if one takes a large enough sample, as for example, the entire Amazon, the number of absolutely very rare species ought to be extremely small because the total abundance of the most common Amazonian tree species is very large.

In contrast, Fisher's logseries makes no such fixed-variance assumption, and the variance in log species abundance increases steadily with increasing sample size. This is because extremely rare species not previously encountered are continually discovered as sample sizes increase, even as previously discovered species become ever more common in the larger samples. In the logseries, the expected number of species ϕ having abundance n is given by

$$\phi(n) = \alpha(x^n/n),$$

where α is a fitted diversity parameter, and x is a parameter whose value is close to but less than unity (if $x > 1$, then the series does not converge). Fisher's α, as parameter α is now known, has become one of the most widely used measures of species diversity because its value changes only slowly in the face of increasing sample sizes of individuals drawn from communities and sorted into species. Why Fisher's α should be relatively constant, and the biological significance of both parameters α and x, was not understood until the development of neutral theory.

APPLYING NEUTRAL THEORY: FISHER'S LOGSERIES OR PRESTON'S LOGNORMAL?

How do we estimate Amazonian tree-species richness and extinction risk due to habitat loss? We can begin by using the framework of neutral theory to estimate the total tree diversity in the Amazonian metacommunity and the expected distribution of relative species abundance and species range sizes. The "metacommunity" refers to the evolutionary–biogeographic unit in which most member species spend their entire evolutionary lifetimes, from origination to extinction, a concept *apropos* to the entire Amazon Basin. Neutral theory generates a biodiversity number θ that uniquely specifies not only how many species are expected to be present at steady state between speciation and extinction in the metacommunity but also the expected abundances of each species. The number θ is a fundamental quantity in neutral theory that is proportional to the product of the average per capita speciation rate in the metacommunity and the size of the metacommunity. Metacommunity size is simply the sum of the population sizes of all species in the metacommunity. An important discovery from neutral theory is that the expected distribution of metacommunity relative species abundance is Fisher's logseries (Hubbell, 2001; Volkov *et al.*, 2003).

The logseries distribution applies in cases when the metacommunity is continuous, as in continental tropical forests, but not necessarily if an island model is more appropriate for the metacommunity, as in the case of isolated coral reefs scattered across the Pacific Ocean (Volkov *et al.*, 2007). Remarkably, it also turns out that the fundamental biodiversity number θ of neutral theory is identical to Fisher's α, the celebrated diversity index of Fisher's logseries, and parameter x of the logseries is the ratio of the average per capita birth rate to per capita death rate in the metacommunity. The reason Fisher's α is so stable, according to neutral theory, is that it is proportional to the average speciation rate in the metacommunity and to the size of the metacommunity, both very stable numbers.

How do we fit Fisher's logseries when the total number of tree species in the Amazon and their relative abundances are unknown? Extensive areas of the Amazon have not yet been adequately collected. Moreover, a large amount of material already collected remains to be described and classified for the first time, and many groups need revision to eliminate synonyms for species described multiple times from collections made by different museums at different times from different parts of Amazonia. Despite current problems with species-level identifications, however, generic-level determinations of Amazonian trees are much more reliable. Most undescribed tree species can at least be placed with reasonable confidence into a known genus. This is fortunate because we can test the fit of the logseries and the lognormal to the abundances of Amazonian genera.

Neutral theory asserts that generic- and familial-level clades should also obey the same metacommunity dynamics as species, the only difference being that they should have lower rates of origination and extinction than species do. Over the last two decades, a dataset comprising over

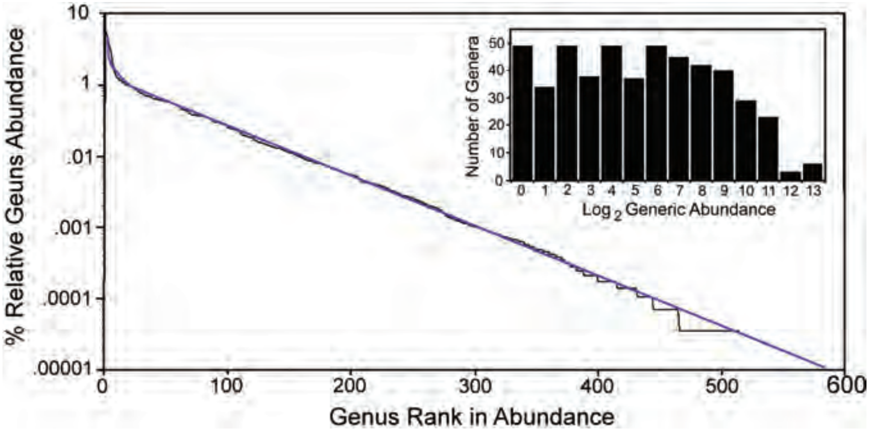

FIGURE 6.2 Fit of Fisher's logseries to the relative abundance data of Amazonian tree genera [(data from ter Steege *et al.* (2006)]. Fisher's α (θ) is ≈71.

a quarter million individual tree records has been assembled by many people from a large number of small plots over the Amazon Basin (ter Steege *et al.*, 2006). The plots extend throughout the Brazilian Amazon into Amazonian Colombia, Ecuador, Peru, and Bolivia to the west and into the Guianan Shield to the northeast. The 288,973 trees have been classified into 514 genera.

The abundances of these genera are fit very well by Fisher's logseries and not by Preston's lognormal (Fig. 6.2). The data are well fit with a value of Fisher's α (θ) of 71. The Preston-style histogram of species binned into doubling classes of abundance (Fig. 6.2 *Inset* graph) has no mode at intermediate abundances and exhibits a flat top as predicted by the logseries in species-rich assemblages but not by the lognormal. Given this result—although we do not yet know the species abundance distribution for the tree flora of the Amazon—it is highly unlikely that the species distribution will be a Preston canonical lognormal. This is different from the prevailing view, which is that tropical lowland forests have low β-diversity and are comprised of relatively widespread common species (Condit *et al.*, 2002) although some dispute this view (Tuomisto *et al.*, 1995).

ESTIMATING THE BIODIVERSITY NUMBER AND ABUNDANCE OF AMAZONIAN TREE SPECIES

Having established that Fisher's logseries and neutral theory give a good fit to the diversity of genera of trees throughout Amazonia, we now need to estimate tree diversity and relative abundance at the species level. The Amazon Basin has ≈50,000 described vascular plant species, in round numbers, of which approximately half are woody. Of these, approximately half are trees, reaching reproductive maturity >10 cm DBH. This yields an estimate of ≈12,500 tree species in the entire Amazon Basin. This is undoubtedly conservative because the number of synonymous species is probably much less than the number of undescribed species. The Brazilian Amazon, which constitutes two-thirds (64.7%) of the entire basin, is expected to have ≈11,210 tree species. This number is what would be expected with an Arrhenius species–area relationship with a z value of 0.25. We can estimate the biodiversity number θ or Fisher's α for all Amazon tree species when we know the number of individual trees in the Amazon. The mean number of trees >10 cm DBH in the 752 plots across the Amazon is 600 ha^{-1}, which translates to 60,000 km^{-2}. The area of the Amazon Basin is 7,179,100 km^2, which yields $4.3075 \cdot 10^{11}$ trees >10 cm DBH. The area of the Brazilian Amazon is 4,468,400 km^2, which gives $2.6810 \cdot 10^{11}$ trees. From the logseries, we have the relationship $S = \alpha \ln(1 + N/\alpha)$, which yields $\alpha = 743$ for the entire Amazon and $\alpha = 500$ for the Brazilian Amazon. These numbers are quite reasonable in light of the estimate of θ for the 50-ha plot in Yasuni National Park in Amazonian Ecuador ($\theta = 212$).

Now that we have estimated the fundamental biodiversity number θ for the Amazon Basin and for that portion of the basin that lies inside Brazil, we can compute the corresponding logseries relative species-abundance distributions. The logseries rank abundance curve for the Brazilian Amazon is shown in Fig. 6.3. The most abundant species has an estimated total abundance of 3.89 billion individuals >10 cm DBH, but despite its abundance, it comprises only 1.393% of all trees. Large numbers of tree

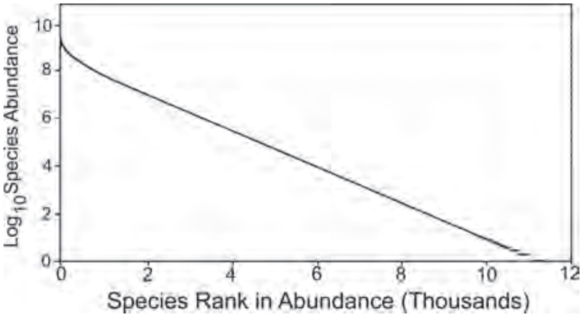

FIGURE 6.3 The predicted logseries rank abundance curve for tree species in the Brazilian Amazon. The size of the metacommunity for this calculation was taken as 4,648,400 km^2 times 60,000 stems >10 cm DBH km^{-2}. The value of Fisher's α (or θ) for this calculation was 500.

species are very abundant; 3,248 species (29.0%) have $>10^6$ individuals in the Brazilian Amazon, and 4,575 species (40.8%) have $>10^5$ individuals >10 cm DBH. At the other end of the relative-abundance spectrum, we estimate that more than a third of all species (3,981, or 35.5%) in the Brazilian Amazon each have (or had) total population sizes $<10^3$ individuals. The remaining quarter of tree species in the Brazilian Amazon have estimated abundances between 10^3 and 10^5 individuals >10 cm DBH.

ESTIMATING THE RANGE SIZES OF AMAZONIAN TREE SPECIES

Many common Amazonian tree species must have extremely large range sizes. In the fertile-soil, aseasonal-climate, high-diversity forests of western Amazonia, many of the same species are found in tree communities separated by thousands of kilometers north and south along the eastern side of the Andes (ter Steege *et al.*, 2006; Condit *et al.*, 2002). One can calculate the probability that two trees randomly sampled from geographically separated tree communities are the same species from existing plot data in western Amazonia. After decreasing rapidly over short distances (<100 m), this probability decays very slowly over large distances (Condit *et al.*, 2002). However, there is much higher turnover of species and genera when one traverses the Amazon Basin over the seasonality gradient from the northwest (aseasonal) to southeast (highly seasonal) and on the soil-fertility gradient from the southwest (high fertility) to the northeast (low fertility) (ter Steege *et al.*, 2006).

Extremely common, widespread species with $>10^6$ adults constitute between a quarter and a third of the total number of Amazonian tree species, and these species are expected to have broad ranges over the Amazon. But what are the range sizes for the many rare to very rare species in the Amazon Basin? By rare in the present context, we mean that the global population size of a given species is small irrespective of the spatial distribution and density of the individual plants of the species. To estimate range size, we need to know the relationship between population size and the area it occupies. If we assume that local population densities of common and rare species are approximately of the same order of magnitude (e.g., because of similar order-of-magnitude seed-dispersal distances), then it follows that rare species will generally have smaller range sizes than common species. This generalization could be violated if rare species are systematically more likely to have a fragmented metapopulation structure than common species.

Whatever the spatial structure of tropical tree populations, however, we can take an empirical approach to this question using the mapped 50-ha plots. We can ask: How does the average distance from a focal tree to a conspecific neighbor change with increasing rank of neighbor, i.e., the distance to the first nearest neighbor, the second nearest neighbor, and so on, to the *n*th nearest neighbor? For a species with a total population size of n individuals, then the average radius of its range will be given by the mean distance to the *n*th nearest neighbor. In taking this approach, one makes no assumptions about the dispersion or degree of species aggregation of tropical tree species, but we know that most tropical tree species are clumped in distribution (Hubbell, 1979; Condit *et al.*, 2000).

In a population with random (Poisson) dispersion, Thompson (1956) proved that the mean distance to the *n*th nearest neighbor r_n is given by

$$E\left[r_n\right] = \frac{1}{\sqrt{\delta}} \frac{n \cdot (2n)!}{(2^n \cdot n!)^2} \approx \frac{1}{\sqrt{\pi\delta}} n^{1/2},$$

where δ is the mean density of trees per unit area. The distance $E[r_n]$ as a function of n is asymptotically a power law for large n. The above approximation is derived from Sterling's formula, which holds very well even for small n. Therefore, the slope of the log–log relationship between distance and rank of nearest neighbor approaches 0.5 as $n \to \infty$ in a Poisson-distributed population. Power laws are convenient because of their scale independence, which means that we can compute $E[r_n]$ for any arbitrarily large population size. But this result was obtained for a randomly distributed population. What about nonrandomly distributed tropical tree populations?

To a very good approximation, the relationship between log $E[r_n]$ and log n is also a power law for nonrandomly distributed tropical tree populations. We computed the relationship between log distance to the *n*th nearest neighbor and log rank of nearest neighbor for all tree species with total abundances $\geq 10^2$ individuals (155 species) in the 50-ha plot on Barro Colorado Island (BCI), Panama. Virtually all of these are very good power laws, illustrated for two arbitrarily chosen species in Fig. 6.4, for all stems >1 cm DBH (Fig. 6.4*a* and *c*) and for canopy adult trees >20 cm DBH (Fig. 6.4*b* and *d*). Based on available data, these power law relationships also appear to hold on spatial scales >>50 ha. For example, *Tabebuia guayacan* (Bignoniaceae), a canopy-emergent species whose individual adults can be accurately censused by using hyperspectral data from the Quickbird satellite, exhibits a very precise log–log relationship over the entire 15.2 km^2 area of BCI (Fig. 6.5) (J.K. and S.P.H., unpublished data). Therefore, we assume that this relationship also holds on larger scales. John Harte has indicated that this result can now be proven (J. Harte, unpublished work). To calculate range sizes of the 11,200 tree species in the Brazilian Amazon, we adjusted the intercept of the log–log regression to reflect the effect of rarity on the first nearest-neighbor distance (Fig. 6.4*f*),

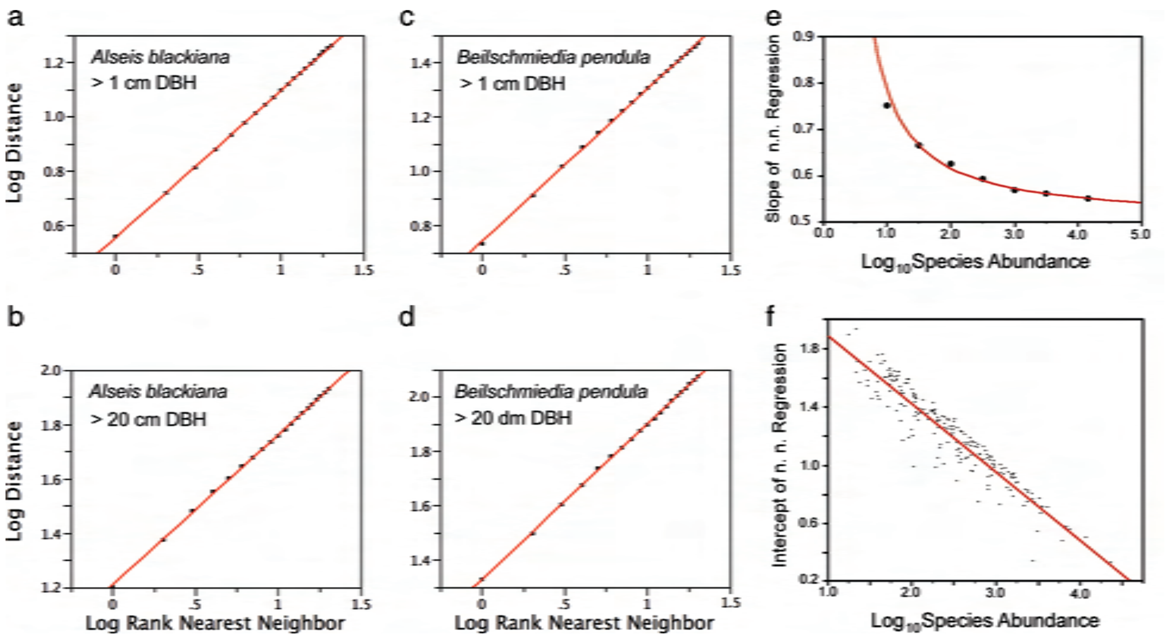

FIGURE 6.4 Log–log relationships between the mean distance to the *n*th nearest conspecific neighbor of a focal plant and the rank of nearest neighbor, for two arbitrarily chosen BCI tree species. (*a*) *Alseis blackiana* (Rubiaceae), stems >1 cm DBH; $Y = 0.5589 + 0.5419X$, $R^2 = 0.999944$. (*b*) *A. blackiana* (Rubiaceae), stems >20 cm DBH; $Y = 1.2137 + 0.5514X$, $R^2 = 0.999376$. (*c*) *Beilschmiedia pendula* (Lauraceae), stems >1 cm DBH; $Y = 0.7472 + 0.5608X$, $R^2 = 0.99951$. (*d*) *B. pendula* (Lauraceae), stems >20 cm DBH; $Y = 1.3328 + 0.5706X$, $R^2 = 0.999638$. (*e*) Distribution of slopes of the log–log relationship between the mean distance to the *n*th nearest conspecific neighbor of a focal plant and the rank of nearest neighbor for the 155 tree species on BCI with abundances $>10^2$. (*f*) Distribution of intercepts for the same relationship.

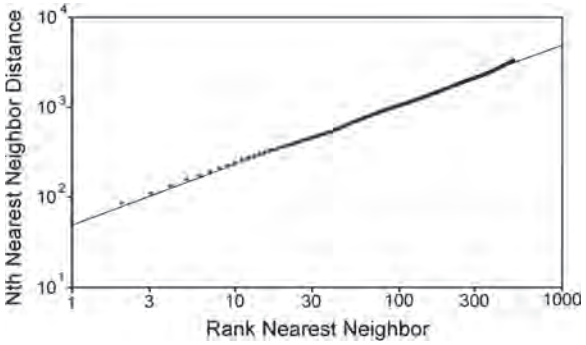

FIGURE 6.5 Landscape-level relationship between the mean distance to the *n*th nearest conspecific neighbor of a focal plant and the rank of nearest neighbor for the rare canopy tree *Tabebuia guayacan* (Bignoniaceae) over the 15.2 km^2 area of BCI, Panama. Power-law relationship for *T. guayacan* adults: $\log_{10}$(distance to *n*th nearest neighbor = 1.7099 + 0.6586 $\log_{10}$(rank nearest neighbor), $R^2 = 0.998$.

and we adjusted the slope based on the inverse relationship between log abundance and the slope (Fig. 6.4*e*).

The predicted mean range sizes in km^2 for species differing in abundance by seven orders of magnitude are listed in Table 6.1. Extremely rare tree species with population sizes $<10^3$ individuals have range sizes <14 km^2 in area. Conversely, at the other end of the abundance spectrum, species with $>10^6$ individuals have range sizes <261,000 km^2. Species with $>10^8$ individuals occupy the entire Amazon Basin. These population and range size calculations are based on the power-law formulae for all individuals

TABLE 6.1 Estimated Tropical Tree Species' Ranges as a Function of Species Abundance in the Brazilian Amazon (total area: 4,652,400 km^2)

Species Abundance	Range Area, km^2	Fraction of Brazilian Amazon
1.0×10^1	2.076×10^{-2}	4.467×10^{-9}
3.0×10^1	9.878×10^{-2}	2.125×10^{-8}
1.0×10^2	5.459×10^{-1}	1.174×10^{-7}
3.0×10^2	2.598×10^0	5.589×10^{-7}
1.0×10^3	1.436×10^1	3.069×10^{-6}
3.0×10^3	6.834×10^1	1.470×10^{-5}
1.0×10^4	3.772×10^2	8.115×10^{-5}
3.0×10^4	1.797×10^3	3.866×10^{-4}
1.0×10^5	9.935×10^3	2.137×10^{-3}
3.0×10^5	4.728×10^4	1.017×10^{-2}
1.0×10^6	2.613×10^5	5.621×10^{-2}
3.0×10^6	1.244×10^6	2.676×10^{-1}
1.0×10^6	1.244×10^6	2.676×10^{-1}

with a stem diameter of >1 cm DBH, with slope and intercept adjusted for species abundance *n* (Fig. 6.4*e* and *f*).

ESTIMATING TREE SPECIES EXTINCTION RISK IN THE BRAZILIAN AMAZON

The area covered by tropical forest in the Brazilian Amazon is still very large, but, partly because it is so large, Brazil is also suffering the highest absolute rate of deforestation of any tropical country in the world. Between 1990 and 1994, the mean annual deforestation rate in the Brazilian Amazon was 1.37 million $\text{ha}\cdot\text{yr}^{-1}$, which increased 61% to 2.20 million $\text{ha}\cdot\text{yr}^{-1}$ a decade later in 2000–2004 (Laurance *et al.*, 2004). This rate of forest loss is equivalent to clearing an area the combined size of the states of Connecticut and Delaware every year. This clearing represents ≈0.43% of the total surface area on the Amazon, not correcting for nonforest area in rivers, lakes, and already deforested portions of Amazonia. When such corrections are applied, conservative estimates of the current rate of deforestation in the Brazilian Amazon are $\approx 0.7\%\cdot\text{yr}^{-1}$.

What is the actual risk of extinction of Amazonian tree species posed by this deforestation in the near term, i.e., over the next several decades? We can now attempt to answer this question, at least to a first approximation, by confronting our calculations of relative species abundance and range sizes with maps of projected loss of forest cover in the Amazon. Detailed maps produced by Laurance *et al.* (2001) consist of two graphical scenarios of the future of the Brazilian Amazon. One scenario they considered "optimistic" (Fig. 6.6*a*) and the other "nonoptimistic" (Fig. 6.6*b*). They evaluated current and pending road-building projects, agricultural development and urbanization, logging, and mining, and then they classified land use into four categories: "heavy-impact areas," "moderate-impact areas," "light-impact areas," and "pristine areas." There is a marked increase in the percentage of area in those four categories of impact, in going from the optimistic to nonoptimistic scenarios. The percentages of area in the four land-use categories under the optimistic scenario were 36.7%, 16.1%, 23.1%, and 24.1%, respectively. Under the nonoptimistic scenario, however, these percentages become: 49.4%, 25.4%, 21.0%, and 4.2%, respectively. For our own analyses, we digitized the maps of Laurance *et al.* at a spatial resolution (pixel size) of 10 × 10-km cells and classified each of these cells into one of the four land-use categories. We limit the analysis to the Brazilian portion of the Amazon because we do not have comparable maps for parts of the Amazon Basin that lie outside Brazil.

Calculating extinction risk for tree species in the Amazon is perhaps the most problematic and the most speculative part of the analysis, but it is a conservation issue of such paramount importance that we feel we

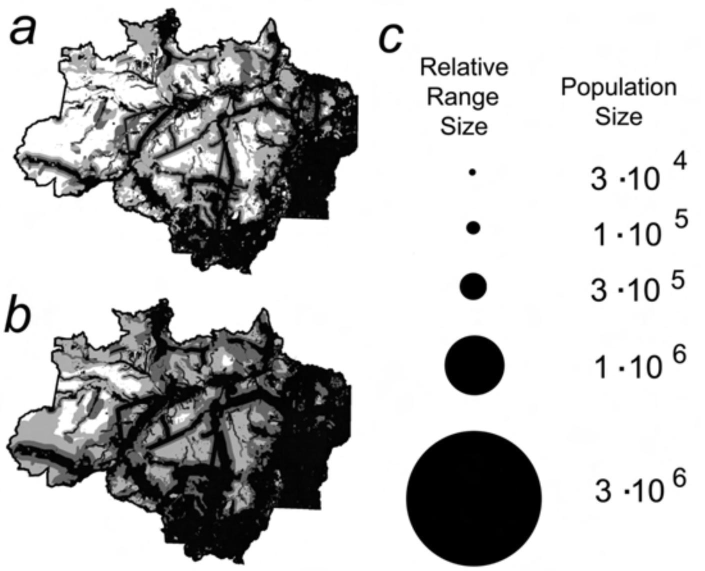

FIGURE 6.6 Scenarios of the future of the Brazilian Amazon [after Laurance *et al.* (2001)]. (*a*) Optimistic scenario. (*b*) Pessimistic scenario. The intensity of shading reflects the relative intensity of human impacts. See text for description of these impacts. (*c*) Relative sizes of species ranges for some highly abundant species, on same scale as maps of the Brazilian Amazon.

must proceed. Whatever the accuracy of our extinction rate estimates, we believe that estimates informed by theory on the distribution of relative tree-species abundance and species range sizes are likely to be more accurate than estimates not based on such information. The two most difficult issues are: (*i*) we do not know where the species whose ranges we can estimate are physically located in the Amazon and (*ii*), perhaps more important, we do not know how each of these tree species will respond to each of the land-use categories.

Faced with these information challenges, we have taken the following approach. With regard to the first problem, the best we can currently do is to perform a large ensemble of stochastic simulations in which we assign locations of all species in the metacommunity randomly throughout the Brazilian Amazon and then average the extinction results over these simulations. In each stochastic simulation, we assigned the centroids of the species ranges at random locations and then calculated the number of pixels of each land-use category that lay within the calculated range size for the species of a given abundance. For species with $<10^2$ individuals, calculated range sizes were smaller than a single pixel, and each of these was assigned to a single pixel of a single land-use category. We then computed the fraction of the species range that was within each land-use category. Range areas were originally calculated as circles whose radii were the mean distances to the *n*th nearest neighbor, but in our simulations, we allowed the compass orientation and shape to vary from circles to ellipses up to a maximum aspect ratio of 4:1 for species whose ranges exceeded 100 km^2 (minimum pixel size), with the long axis at a random angle with respect to north. The relative sizes of the Brazilian Amazon and some of the larger species range sizes are shown in Fig. 6.6*c* on the same scale as the maps in Fig. 6.6*a* and *b*.

With regard to the second problem—the responses of species to the land-use categories—we have run three extinction scenarios, the first of which we believe is most likely. The first scenario obeys a middle-of-the-road conservative rule of the three extinction scenarios—conservative in the magnitude of predicted extinction rates. The rule is that a species goes extinct if, and only if, its range lies entirely in heavy-impact areas. Of the four land-use categories, the heavy-impact areas, are most likely to result in tree extinctions among species restricted to these areas because they have lost virtually all of their primary forest cover, and what forest remains is in very small, isolated, and highly disturbed remnants.

Although speculative, we think is it likely that the other land-use categories will have minimal impact on elevating species extinction above background rates. Despite the visually alarming appearance of the nonoptimistic scenario map (Fig. 6.6*b*), the descriptions of the land-use categories in online supplementary material to the paper by Laurance *et al.* (2001) do not describe impacts that are likely to cause many, if any, tree-species extinctions, in our opinion. For example, light-impact areas still retain nearly intact primary forest cover (>95%) but can "experience illegal gold-mining, small-scale farming, hunting, hand-logging, and nontimber resource extraction (e.g., rubber-tapping)." Even moderate-impact areas still have mostly intact primary forest cover (>85%) but "contain localized forest clearings and some roads, and may be affected by logging, mining, hunting, and oil and gas exploration." The fourth land-use category, pristine, is, by definition, the reference or "natural" state in which extinction occurs at background rates. These areas are described as having "fully intact primary-forest cover and are free from anthropogenic impacts aside from limited hunting, fishing, and swidden farming by traditional indigenous communities."

One can, however, erect a plausible second extinction scenario in which species could go extinct in moderate-impact areas at a higher than background rate, and even in light-impact areas. This is potentially the least conservative scenario, the one that predicts the most extinctions.

Because the land-use categories are broad averages, they can potentially obscure local heterogeneity in the rate of loss of forest cover, so it is conceivable that a rare, localized endemic species may be eliminated in one of the cleared areas. In our second scenario, species still go extinct if their range lies entirely in heavy-impact areas. However, they can also go extinct if they have ranges that lie partially or wholly within moderate- or light-impact areas. The second-scenario rule is that there is a 15% probability of extinction of each cell occupied by the species in the moderate-impact zone (because there is a 15% loss of forest cover in these areas) and a 5% probability of extinction of each cell occupied in the light-impact zone (because there is a 5% loss of forest cover in these areas). These "coin tosses" per cell are assumed to be independent Bernoulli trials, so the probability of a joint event is the product of the per-cell probabilities. If the species has no range in the unimpacted areas, and if it goes extinct in all of the cells it occupies in light- and moderate-impact areas (and it goes extinct in all heavy-impact cells), then the species goes globally extinct.

The third scenario is at the other extreme, the most conservative hypothesis, predicting the lowest extinction rates. This scenario says that even if a species is restricted to the heavy-impact zone, it has a nonzero chance of surviving. It is difficult to know what survival probability to give a species, but we assume that the larger the range of the species (more individuals), the greater the chance that some local population will survive in one of the forest fragments. For sake of argument, we assume in this scenario that a species has a 5% chance of surviving per heavy-impact cell occupied. One could run many different versions of this scenario with different survival probabilities. A species whose range lies entirely within the heavy-impact zone could nevertheless survive if it survives in at least one of the heavy-impact cells it occupies.

Given these extinction scenarios, what are the predicted extinction rates? Fig. 6.7*a* shows the results for the middle-of-the-road extinction scenario 1. The qualitative pattern is that the probability of extinction is a logistic function of species abundance (range size), with high extinction probabilities for rare species, dropping to essentially zero probability for species above a critical population-size threshold of $\approx 10^6$ individuals. Below population sizes of $\approx 10^4$ individuals, the mean probability of extinction is close to the proportion of heavy-impact areas under Laurance *et al.*'s (2001) optimistic and nonoptimistic deforestation scenarios. This result is not unexpected because predicted range sizes of tree species with $<10^4$ individuals are small, <24 km^2. Under the nonoptimistic deforestation scenario 3,656 tree species (32.6%) are predicted to go extinct, but only 354 of these species have population sizes of $>10^5$ individuals, and only 42 species predicted to go extinct have population sizes of $>10^6$ individuals. But even under the optimistic deforestation scenario, 2,228 tree species

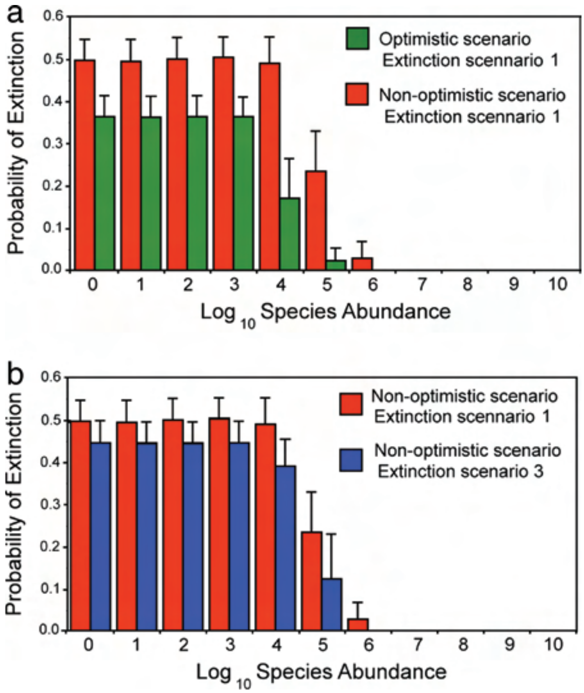

FIGURE 6.7 Predicted extinction rates of tree species in the Brazilian Amazon under the optimistic and nonoptimistic scenarios of Laurance *et al.* (2001) as a function of population size. The abundance bins (histogram bars) are labeled with the logarithm to the base 10 of the lower bound of abundance in the respective bin. (*a*) Extinction scenario 1: Species go extinct only if their entire geographic range is in heavy-impact areas (in Fig. 6.6) on either the optimistic or the nonoptimistic scenarios of Laurance *et al.* (2001). (*b*) Comparison of extinction scenarios 1 and 3. In extinction scenario 3, species manage to survive in heavy-impact areas if at least one occupied cell survives, with probability 0.05 per cell. Extinction scenario 2 (data not shown), in which species can go extinct if they have some portion of their range in areas other than heavy-impact, gave results very similar to extinction scenario 1

(19.9%) are predicted to go extinct, of which 36 species have population sizes of $>10^5$ individuals. However, for the 3,248 species (29.0%) with $>10^6$ individuals apiece, there are no forecast extinctions under the optimistic scenario.

Extinction scenario 2 (results not shown) gave qualitatively similar results to scenario 1 because we made it hard to go extinct in moderate- to light-impact areas (all occupied cells in these areas had to go extinct, with fairly low probability of extinction in each cell: 15% and 5% per-cell extinction probability in moderate- and light-impact areas, respectively).

Extinction scenario 3 showed a significant "rescue effect" relative to scenario 1 for species with population sizes between 10^3 and 10^5 (Fig. 6.7*b*) even though the probability of survival of species in heavy-impact areas was small on a per-cell basis. A total of 3,085 species (27.5%) are expected to go extinct under extinction scenario 3, which is 571 fewer species than under extinction scenario 1, under the pessimistic case. There is also an ≈3% improvement in the mean survival of species with $<10^3$ individuals, but the extinction rate of these rare species is still very high, <47%.

One question we cannot answer is how many of these extinctions have already taken place. At the time this chapter was written, we did not have a map of areas already deforested in the Brazilian Amazon. It is quite clear that much of the Atlantic forest in Amazonia is already gone. This fact is reflected by the scant change in heavy-impact areas in the eastern Amazon between the maps for the optimistic and nonoptimistic deforestation scenarios. Thus, our estimates of extinction rates due to future deforestation are likely to be overestimates because they include species that have already gone extinct.

CONCLUSIONS AND CAVEATS

A controversy in recent years has been developing over the future of the Amazon. On the one side are scientists legitimately concerned with the rapid deforestation of the Amazon and the potential consequences for not only species extinction but also for the loss of ecosystem services, such as climate amelioration, soil conservation, and the welfare of wildlife and other species that depend on the trees for their survival (Laurance *et al.*, 2001, 2002, 2004; Brooks *et al.*, 2002). On the other side, however, are scientists who believe that the short-term extinction threat, particularly from human population growth, is greatly exaggerated, and that rates of deforestation are likely to decline in the future (Wright and Muller-Landau, 2006a,b). In retrospect, many of the predictions of tropical deforestation made in the 1970s and 1980s have not come to pass (Myers, 1980). For example, the eminent tropical forest ecologist and biogeographer, T. C. Whitmore (1980) wrote, nearly three decades ago, that "the onslaught [on tropical forests] will continue to accelerate, reducing the forest to scattered fragments by A.D. 2000." Although he was wrong on his dates, if one takes a longer view, one may worry that Whitmore's dark vision will prove to be accurate.

The results of the present analysis paint a somewhat more complex and nuanced picture of the future of Amazon forests and its tree species. On the one hand, under all of the scenarios we considered, a large number of very common tree species will almost certainly survive habitat losses, whether one takes an optimistic or nonoptimistic view of deforestation in the Brazilian Amazon. This is the good news. However, it is not clear how many survivors of habitat loss will also survive the novel climates forecast for the Amazon, which include significantly warmer temperatures and more variability in rainfall, accompanied by longer and more severe droughts (Williams *et al.*, 2007). The bad news is that large percentages of rare and endemic species will probably go extinct. The number of rare tree species at risk of extinction from habitat loss could be in the hundreds to several thousand. The actual number at risk is uncertain, because it depends on how many rare species really exist in the Amazon.

There are many caveats to this analysis. A central issue is whether Fisher's logseries is the correct model of relative tree-species abundance in the Amazon tree metacommunity. This assumption leads to the prediction of high species richness and many rare species and high extinction rates of rare species. In defense of the theory, there is strong support in the data on tree-species abundances across Central Panama (data not presented), and from the abundances of tree genera across Amazonia, that the logseries is the right model.

Another caveat is that the analysis considers only tree-species extinctions and not the potential extinction of other animal and plant (microbial?) species, that are likely to accompany habitat loss. There are also many complex biological interactions in tropical rainforests affecting the survival and reproduction of tropical tree species that might be seriously impacted by forest degradation long before complete deforestation occurs. For example, many tropical trees are bat-pollinated, and their successful reproduction depends on bats. What do we know about the susceptibility of bat communities to forest fragmentation?

Another issue is that the calculation of the number of tree species at risk also depends on how individual species will respond to different levels of forest disturbance and conversion. This unknown is undoubtedly the most challenging aspect of the present analysis. Although it is an old scientific chestnut, we must once again emphasize how important it is to support continuing basic science on tropical forests. We urgently need information on the biogeography, population sizes, comparative life histories, and environmental requirements of tropical tree species. As such data accumulate, we can not only make more accurate assessments of extinction risks, but also have more informed and intelligent suggestions for how to save tropical tree species and forests from extinction.

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7

Microbes on Mountainsides: Contrasting Elevational Patterns of Bacterial and Plant Diversity

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The study of elevational diversity gradients dates back to the foundation of biogeography. Although elevational patterns of plant and animal diversity have been studied for centuries, such patterns have not been reported for microorganisms and remain poorly understood. Here, in an effort to assess the generality of elevational diversity patterns, we examined soil bacterial and plant diversity along an elevation gradient. To gain insight into the forces that structure these patterns, we adopted a multifaceted approach to incorporate information about the structure, diversity, and spatial turnover of montane communities in a phylogenetic context. We found that observed patterns of plant and bacterial diversity were fundamentally different. While bacterial taxon richness and phylogenetic diversity decreased monotonically from the lowest to highest elevations, plants followed a unimodal pattern, with a peak in richness and phylogenetic diversity at mid-elevations. At all elevations bacterial communities had a tendency to be phylogenetically clustered, containing closely related taxa. In contrast, plant communities did not exhibit a uniform phylogenetic structure across the gradient: they became more overdispersed with increasing elevation, containing distantly related taxa.

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Finally, a metric of phylogenetic beta-diversity showed that bacterial lineages were not randomly distributed, but rather exhibited significant spatial structure across the gradient, whereas plant lineages did not exhibit a significant phylogenetic signal. Quantifying the influence of sample scale in intertaxonomic comparisons remains a challenge. Nevertheless, our findings suggest that the forces structuring microorganism and macroorganism communities along elevational gradients differ.

Roughly 250 years ago, Carolus Linnaeus (1781) documented how distinct plant and animal communities characterized the succession of climatic zones along the slopes of mountains. Such elevational gradients are characterized by dramatic changes in climate and biotic turnover over short geographic distances. The patterns observed by Linnaeus and his contemporaries played a foundational role in the development of ecology and biogeography (Briggs and Humphries, 2004). Studies of how individual taxa and community composition respond to elevational gradients have led to a search for generalized elevational patterns of biodiversity (Brown, 2001; Lomolino, 2001; McCain, 2005). These studies have documented elevational patterns of diversity across a wide variety of taxonomic groups, including trees, mammals, birds, reptiles, insects, and amphibians. In sum, this work has shown that taxa generally exhibit either monotonically decreasing or hump-shaped richness patterns with elevation (Stevens, 1992; Rahbek, 2005). However, despite a large number of proposed hypotheses to explain elevation patterns of diversity, their causes remain poorly understood. Improved knowledge of elevation gradients is fundamental to advancing basic ecology and predicting the potential consequences of climate change. Species in montane regions are often cited as being very sensitive to the impacts of warming (McDonald and Brown, 1992; Parmesan, 2006; Thuiller, 2007).

Although elevational patterns of diversity for plants and animals are well established, we know very little about how microbial diversity varies across elevational gradients. This is a serious gap in our general understanding of biodiversity, given that microbes are abundant and diverse, play a central role in ecosystem functioning, and will likely be an important component of ecosystem response to global warming (Rillig *et al.*, 2002; Monson *et al.*, 2006; Carney *et al.*, 2007). Elevational diversity studies that consider empirical patterns of macroorganisms and microorganisms in parallel are needed to provide a more unified framework for understanding diversity patterns in Earth's major environmental gradients and predicting systemwide ecological responses to climatic change.

Traditional elevational diversity studies have focused on how patterns of species richness, abundance, and range size change with altitude. These analyses have used a nomenclatural approach by focusing on species identities. However, the increasing availability of molecular phylogenies has renewed interest in using phylogenetic approaches to study the forces that influence patterns of biodiversity and biogeography [e.g., Chave *et al.* (2007)]. Because many species traits are generally conserved during the evolution of a lineage, one would expect a positive relationship between a measure of the phylogenetic relatedness of two species and a measure of their overall ecological similarity (phylogenetic niche conservatism) (Harvey and Pagel, 1991). As a result, analysis of the degree of phylogenetic relatedness of taxa found within and across communities should provide insight into the ecological and evolutionary processes that organize these communities.

Here, in an effort to assess the generality of elevational diversity patterns and the forces that structure these patterns, we quantified both plant and soil bacterial diversity patterns along an elevational gradient in the Colorado Rocky Mountains. A parsimonious hypothesis is that if the forces structuring biodiversity across the gradient are the same for bacteria and plants, then the resulting taxon and phylogenetic biogeographic patterns will be similar for both groups. Alternatively, if ecological and evolutionary processes along elevational gradients differ between the two groups (e.g., the taxa differ in their dispersal ability, response to environmental heterogeneity, interspecific interactions, or speciation rates), then we would expect them to be characterized by distinct patterns of diversity. To test these hypotheses, we adopted a multifaceted approach that examines diversity in the context of both ecological and evolutionary patterns. Therefore, in addition to the established convention of quantifying patterns of taxon richness and taxon turnover along the gradient [e.g., Whittaker (1960, 1967)], we examined several biodiversity measures that incorporate information about the phylogenetic structure, phylogenetic diversity, and phylogenetic turnover of plant and bacterial communities.

ELEVATIONAL DIVERSITY IN A PHYLOGENETIC CONTEXT

While the sampling methods and taxonomy used to quantify plant diversity are well established and standardized, microbial surveys vary greatly in their approach to characterizing diversity (Eisen, 2007). We determined the bacterial community composition of our soil samples by analyzing a PCR-amplified region of 16S ribosomal DNA, the most commonly used indicator of microbial biodiversity. Because bacteria are overwhelmingly diverse in soils, we chose PCR primers that narrowed our focal group to the phylum *Acidobacteria*. This subgroup of bacteria is diverse and ubiquitous in soils (Janssen, 2006) and thought to play an important role in biogeochemical cycling (Eichorst *et al.*, 2007).

We followed the classic approach to intertaxonomic diversity analysis by comparing patterns of species richness and phylotype richness of plants and bacteria, respectively, along the gradient. We also quantified the phylogenetic diversity of every sampled community by calculating the sum of the branch length in a phylogeny that connects all species in a community and the root (Faith, 1992b). Phylogenetic diversity is more inclusive than a simple count of species or types, in that it quantifies the evolutionary history of a group of taxa (Vane-Wright *et al.*, 1991). Conservation biologists are interested in preserving phylogenetic diversity, as this is fundamental to maximizing evolutionary options for the future (Faith, 1994; Myers and Knoll, 2001; Sechrest *et al.*, 2002; Forest *et al.*, 2007). Phylogenetic diversity is also believed to correspond to "feature diversity," meaning the number of evolutionarily derived traits within a biological community (Faith, 1992b).

In addition to measuring phylogenetic diversity, we quantified community phylogenetic structure along the gradient by using two commonly used metrics: a mean pairwise distance metric sensitive to phylogeny-wide patterns [net relatedness index (NRI)] and a nearest-taxon-based measure sensitive to patterns at the "tips" of the phylogeny [nearest taxon index (NTI)] (Webb *et al.*, 2002). The degree of phylogenetic relatedness quantified by these metrics provides insight into drivers of community assembly. Assuming phylogenetic niche conservatism, phylogenetic clustering within a local assemblage is considered consistent with the hypothesis that selective filters (e.g., environmental conditions) cause local assemblages to comprise closely related taxa (Webb *et al.*, 2002). Phylogenetic overdispersion, on the other hand, can be explained by two possible biotic interactions: competition (Webb *et al.*, 2002) or facilitation (Lortie, 2007; Valiente-Banuet and Verdu, 2007). In the case of competition, more closely related species are hypothesized to compete more strongly with one another. This results in competitive exclusion, which leads to a community of distantly related species. In the case of facilitation, facilitator species are hypothesized to create microhabitats that permit distantly related species adapted to different environments to persist within a local assemblage.

In addition to considering patterns in the diversity and phylogenetic structure within communities along the elevation gradient (alpha-diversity), we investigated how community composition changes across a landscape (beta-diversity). Ecologists have long recognized that beta-diversity is important for understanding the biodiversity of montane ecosystems (Jaccard, 1912; Whittaker, 1960; Harte *et al.*, 1999; Brehm *et al.*, 2003; Mena and Vazequez-Dominguez, 2005). We examined beta-diversity in terms of compositional similarity, defined as the fraction of taxa shared between two samples (Sørensen index), and phylogenetic similarity, defined as the fraction of branch lengths shared between two samples. By analogy with the well-established distance–decay relationship, which describes the decrease in compositional similarity between two communities with increasing geographic distance (or equivalently elevational separation) between them (Soininen *et al.*, 2007), we described the decrease in phylogenetic similarity with distance (phylogenetic distance–decay). Our objective in exploring both measures of beta-diversity is to understand not only if there are shifts in compositional similarity with increasing elevational distance, as expected along an environmental gradient, but to quantify the phylogenetic nature of the shifts.

Phylogenetic similarity reflects the combined additive influence of: (*i*) lineages that are shared between two communities that lead to shared taxa, and (*ii*) lineages that are shared but ultimately lead to unshared taxa. One can test whether the phylogenetic similarity between two communities is solely a consequence of compositional similarity, or if it is also caused by a nonrandom structure of shared and unshared lineages. A significant phylogenetic distance–decay pattern (i.e., one that differs from that expected by taxa turnover alone; see *Materials and Methods*) reflects significant spatial variability in lineage composition across a landscape. Based on the assumption of phylogenetic niche conservatism described above, changes in lineage composition should correspond to changes in the traits of species. Under this model, a significant phylogenetic distance–decay relationship should reflect strong variability in the ecologically relevant traits of biological communities across a landscape.

RESULTS AND DISCUSSION

Whereas bacterial richness decreased monotonically from the lowest to highest elevations, plant richness followed a unimodal pattern with a peak in species richness at midelevations (Fig. 7.1*A*). These contrasting diversity patterns emerged when richness values were calculated for bacterial and plant samples individually and also when the samples for each respective group were pooled together at every elevational band [following the protocol suggested by Whittaker (1960)]. To our knowledge, an altitudinal richness pattern has never been reported for microorganisms. The patterns observed here for microbes and plants are consistent, respectively, with the classical monotonically decreasing and hump-shaped patterns observed across most macroorganism groups (Stevens, 1992; McCain, 2005; Rahbek, 2005). It has been argued that these two contrasting richness patterns may emerge as a result of inconsistent sampling approaches among different studies, rather than an underlying ecological mechanism (Lomolino, 2001; Rahbek, 2005). By implementing a parallel sample design for the bacteria and plants, we controlled for two potential biases: varia-

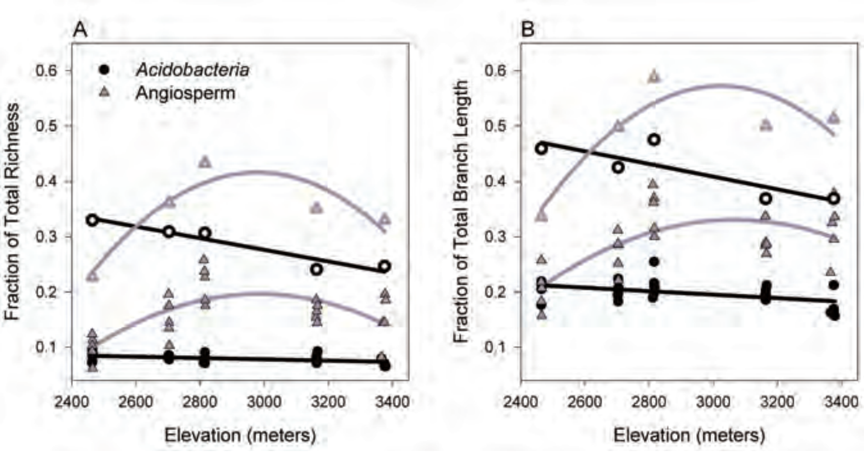

FIGURE 7.1 Variation in taxon richness (*A*) and phylogenetic diversity (*B*) across the elevation gradient. Data are presented as the fraction of total richness and phylogenetic diversity across the gradient. Solid symbols indicate sample richness (core or quadrat), and open symbols indicate the pooled richness at each elevational site (n = 5 per site). At the sample level, *Acidobacteria* richness and phylogenetic diversity linearly decrease with elevation (regression analysis, $r^2 = 0.22$, $P < 0.05$; $r^2 = 0.23$, $P < 0.05$, respectively), whereas angiosperm richness and phylogenetic diversity patterns are hump-shaped (regression analysis, $r^2 = 0.53$, $P < 0.0005$; $r^2 = 0.47$, $P < 0.005$, respectively). Model choice was based on Akaike information criteria.

tion in sampling extent (i.e., the geographic distance between the furthest sampled elevations), which often occurs among studies, and sampling intensity (or effort) along the gradient within a taxonomic group, which often occurs within studies. As a result, the disparity in elevational richness patterns observed between bacteria and plants is likely caused by differences in how ecological and evolutionary processes have operated across the gradient (although see below for a discussion on the potential influence of scaling effects).

As expected, for both bacteria and plants (Forest *et al.*, 2007) we found that the patterns of phylogenetic diversity mirrored those of taxon richness (Fig. 7.1*B*). However, a more detailed look at the phylogenetic structure of the bacterial and plant communities revealed another significant difference. At all elevations bacterial communities had a tendency to be more phylogenetically clustered than expected by chance (Fig. 7.2). This observation is consistent with results reported by Horner-Devine and Bohannan (2006) who found that bacterial communities in a wide range of environments tended to be phylogenetically more closely related than expected

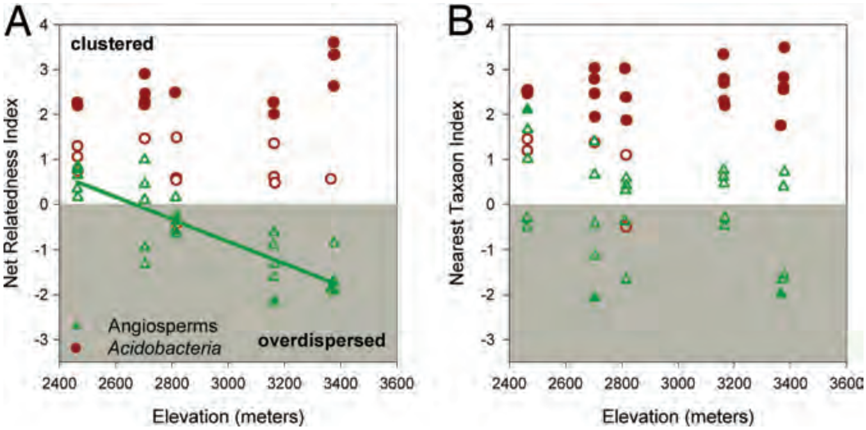

FIGURE 7.2 Variation in community phylogenetic relatedness along the elevation gradient as measured with the NRI (*A*) and NTI (*B*). Positive index values indicate phylogenetic clustering, and negative values indicate phylogenetic overdispersion. Observed community phylogenetic structures unlikely to arise by chance ($P < 0.05$) are depicted by solid symbols. All microbial communities are clustered, with >50% being significantly clustered. Angiosperm communities are not uniformly clustered or dispersed across the gradient, but rather become increasingly overdispersed with increasing elevation. This trend in increased overdispersion with elevation is significant when measuring relatedness with the NRI (solid line; $r^2 = 0.70$, $P < 0.001$).

by chance. Given the parsimonious hypothesis that closely related taxa are more ecologically similar (i.e., phylogenetic niche conservatism), our results suggest that abiotic filtering tends to be a more prominent force in the structuring of bacterial communities along the gradient. Several studies have suggested that for most macroorganisms, ecological traits are phylogenetically conserved (Prinzing *et al.*, 2001; Blomberg *et al.*, 2003; Cavender-Bares *et al.*, 2004). It is important to emphasize that although this statement may be correct for macrorganisms, the generality of niche conservatism for microorganisms and in particular bacteria is unknown. Observed phylogenetic clustering in microbial communities could also be the result of radiation events combined with dispersal limitation (Horner-Devine and Bohannan, 2006). As we discuss below, alternative explanations for the patterns we observe relate to the phylogenetic and spatial scale of our analyses (Swenson *et al.*, 2006, 2007). Scaling issues are relevant to all of the biodiversity patterns we examined.

In contrast to bacteria, plant communities did not show a uniform phylogenetic structure across the gradient. Plant communities tended to exhibit either random phylogenetic structure or phylogenetic overdispersion. Surprisingly, our analyses indicated that plant communities also tended to become increasingly overdispersed at higher elevations (Fig. 7.2). Given niche conservatism, phylogenetic overdispersion is consistent with the importance of biotic forces (competitive exclusion or facilitation) structuring community diversity. Recent experimental evidence suggests that both of these forces are important drivers in alpine plant community assembly, with a shift from competition at lower elevations, where conditions are less physically stressful, to facilitation at higher elevations where abiotic stress is high (Callaway *et al.*, 2002). Increased overdispersion at high elevations suggests that the influence of facilitation on high-elevation communities is stronger than the influence of competition at low elevations. An alternative explanation is that the evolution of traits necessary to cope with environmental conditions at high elevations has occurred independently in distantly related lineages (i.e., convergent evolution in high alpine plants) (Webb *et al.*, 2002). This explanation goes against the assumption of phylogenetic niche conservatism.

We observed that both plant and bacterial compositional similarity significantly decreased with elevational distance (Fig. 7.3). Plant and bacterial communities differed, however, in their phylogenetic distance–decay patterns. The bacterial phylogenetic distance–decay curve was significantly steeper than expected from the observed bacterial taxa turnover alone (Fig. 7.3*A*). In contrast, the plant phylogenetic distance–decay curve was not significantly different from expected from the observed decay in plant compositional similarity. These results are consistent with those reported above for the NRI and NTI measures of community phylogenetic structure, indicating that bacteria lineages were not randomly distributed across the elevation gradient. Rather, bacterial lineages exhibited a spatially structured pattern across the gradient. Given the parsimonious hypothesis that closely related taxa are more ecologically (or functionally) similar, our observations suggest that bacterial lineages harbor increasingly disparate ecological features (or functions) at increased elevational distances as a probable consequence of abiotic filtering. These findings highlight the utility of gathering information on phylogenetic relationships between communities in montane regions as a means to quantify the potential consequences of selectively trimming evolutionary lineages under the scenario of mountaintop extinctions in response to global warming.

Although our study was not designed to directly examine the environmental drivers of elevational diversity patterns, our results do illuminate their potential role in shaping biodiversity patterns across the gradient. The contrasting phylogenetic diversity patterns we observed in plants and microbes suggest a differing role in how abiotic forces structure communities across the gradient. Soil temperature and pH were consis-

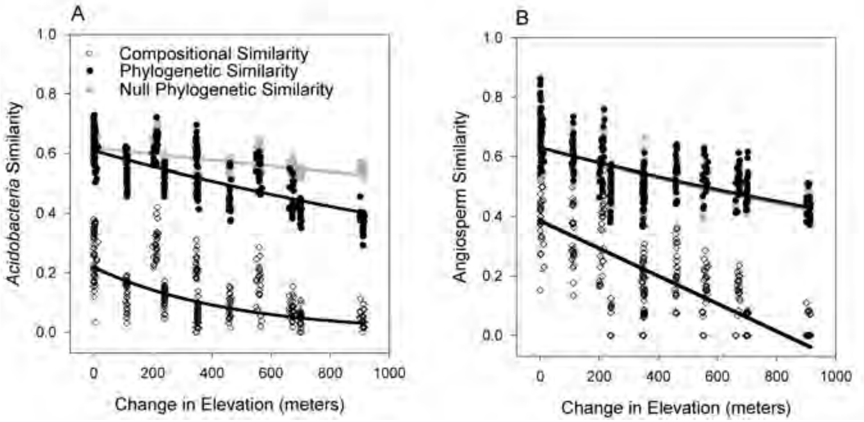

FIGURE 7.3 Compositional and phylogenetic similarity of *Acidobacteria* communities (*A*) and angiosperm communities (*B*), as a function of the elevation separating the communities. The compositional (hollow black triangle) and phylogenetic (solid black circles) similarity for both angiosperm and *Acidobacteria* communities significantly decrease with increasing elevational separation (Mantel test, $P < 0.001$). Lines represent best-fit regressions of similarity versus change in elevation (see *Materials and Methods*). The slope of the decay of phylogenetic similarity between *Acidobacteria* communities is significantly steeper than predicted by a null model constrained by the decrease in taxon turnover (solid gray circles) ($P < 0.05$). The slope of the decay in phylogenetic similarity across the angiosperm communities is not significantly different from the null prediction given species turnover.

tently correlated with diversity in both plants and bacteria, and bacterial diversity was also strongly correlated with slope in a univariate analysis (Table 7.1). A multivariate analysis suggested that soil temperature was the major explanatory variable of taxon richness and phylogenetic diversity for both plants and bacteria ($P < 0.001$ in six of eight multivariate models). Turnover in taxon and phylogenetic composition of plant and bacterial communities was significantly correlated with changes in the majority of our measured environmental parameters (7.2); however, the combined influence of soil temperature, pH, and total nitrogen was the most important predictor for both groups. After controlling for these environmental parameters, geographic distance between samples significantly correlated with all turnover patterns (partial Mantel test, $P < 0.001$). These results imply that dispersal limitation could be occurring, but given the small geographic range of our gradient, they are more likely caused by effects of environmental heterogeneity that we did not characterize. The correlation of richness and turnover with temperature and pH is consistent with the

TABLE 7.1 Pearson Correlation Coefficients from Univariate Models Predicting Alpha Diversity Measures as a Function of Environmental Parameters

Diversity Type	Elevation	Temperature	pH	Slope	Aspect	% Nitrogen	% Carbon	% Moisture
Microbial richness	–0.222*	0.174*	0.205*	–0.239*	0.044	–0.002	0.0002	–0.148
Plant richness	_0.533_***	_–0.502_***	–0.189*	0.004	0.039	_0.271_	0.077	0.045
Microbial phylogenetic diversity	–0.228*	0.216*	0.132	_–0.311_*	0.030	–0.0001	_0.116_	–0.0009
Plant phylogenetic diversity	_0.473_**	_–0.443_**	–0.283*	0.069	0.002	_0.229_	0.022	0.056
Microbial NRI	0.056	–0.063	–0.025	_0.227_	0.018	0.037	0.0001	0.002
Plant NRI	–0.696***	0.699***	0.536***	–0.411**	0.132	_0.094_	0.056	0.001
Microbial NTI	0.101	–0.120	–0.054	0.048	–0.008	0.0004	–0.233	–0.026
Plant NTI	–0.109	0.109	–0.015	–0.015	0.002	–0.059	–0.037	–0.004

For each environmental parameter both a linear and a quadratic model were fit. The best fit model was chosen using the lowest Akaike Information Criterion (AIC) value (see *Materials and Methods*). Quadratic models are indicated with *italics*, and a minus sign (–) is used to indicate the

TABLE 7.2 Mantel Correlations Between Community and Environmental Similarities

	Elevation	Temperature	pH	Slope	Aspect	% Nitrogen	% Carbon	% Moisture
Acidobacteria compositional similarity[a]	–0.57**	–0.57**	–0.64***	–0.19*	–0.10	–0.32**	–0.17*	0.17*
Acidobacteria phylogenetic similarity[b]	–0.78	–0.76**	0.76**	–0.40**	–0.24*	–0.18*	–0.06	–0.04
Angiosperm compositional similarity[a]	–0.69**	–0.72**	–0.44**	–0.24*	–0.26*	–0.33*	–0.25*	–0.07
Angiosperm phylogenetic similarity[b]	–0.65**	–0.65**	–0.37**	–0.16	–0.19	–0.38*	–0.27*	–0.23*

[a] Quantified with Sørensen index.

[b] Quantified with PhyloSor. $*P \leq 0.05$, $**P \leq 0.005$.

findings of other studies of plant (Allen *et al.*, 2002; Hawkins *et al.*, 2003; Currie *et al.*, 2004) and microbial (Fierer and Jackson, 2006) diversity.

It is well documented that the scale over which biodiversity is sampled will strongly influence observed patterns. For example, recent empirical studies have shown that decreasing the spatial grain at which organisms are sampled shifts their diversity patterns (Rahbek, 2005; Cavender-Bares *et al.*, 2006; Slingsby and Verboom, 2006; Swenson *et al.*, 2006, 2007). Although the spatial extent of our study was the same for bacteria and plants, the grain of our sample observations was different between these two groups. The spatial scales over which bacteria interact with each other are likely to be several orders of magnitude smaller than the scale at which they were sampled. Therefore, relative to plants, bacteria were likely sampled at a coarser grain, and thus we may have included a greater amount of environmental heterogeneity within a bacterial sample. Sampling bacteria at a spatial scale that more closely approaches the "ecologically equivalent" grain of plants may result in convergent biodiversity patterns between these two groups.

Taxonomic scale also influences biodiversity patterns. For example, taxonomic breadth, which defines how broadly or narrowly a target community is defined from a phylogenetic perspective (e.g., bacteria versus *Acidobacteria*), can shift the degree of observed overdispersion or clustering in that community (Swenson *et al.*, 2006). Species are a natural taxonomic unit by which to measure plants (Mayr, 1942). Such an intuitive unit does not exist for prokaryotes. In this study we classified partial *Acidobacteria* 16S ribosomal DNA sequences into taxonomic units based on the commonly used 99% sequence similarity designation (see *Materials and Methods*). It is unknown how taxonomic resolution, defined as the threshold at which individuals are binned into taxonomic units, should influence phylogenetic patterns, although it has been shown to impact taxonomic patterns such as the taxa–area relationship (Horner-Devine *et al.*, 2004b). We found that binning bacteria into increasingly broader taxonomic units (i.e., 97%, 94%, and 90% sequence similarity) tended to dampen the strength of all observed elevational diversity patterns. However, general trends did not qualitatively change (Figs. 7.4–7.6), suggesting that taxonomic resolution is not the cause of disparate bacterial and plant biodiversity patterns in this study. Alternative approaches to defining bacterial taxonomic units such as "ecotypes" (Cohan and Perry, 2007) could significantly change the results and lead to plant and microbial diversity patterns that more resemble one another.

Differences in the approach to building the *Acidobacteria* and angiosperm phylogenetic trees should also be considered when comparing phylogenetic patterns between these two groups. The *Acidobacteria* phylogeny was estimated solely from molecular data identified in this study, whereas

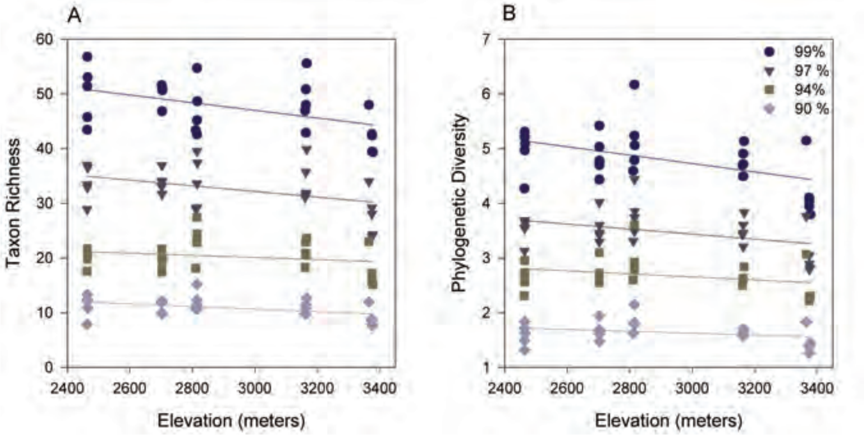

FIGURE 7.4 Variation in *Acidobacteria* (*A*) taxon richness and (*B*) phylogenetic diversity across the elevation gradient at four different taxonomic resolutions. Taxonomic richness is the total number of taxa (phylotypes) and phylogenetic diversity is the minimum total branch length connecting all taxa in the community and the root. Richness and phylogenetic diversity are best modeled as linearly decreasing with elevation at all taxonomic resolutions (Akaike information criteria). Slopes of the taxon richness patterns: 99%, –0.006982*; 97%, –0.005158*; 94%, –0.001939; 90%, –0.002364*. Slopes of the phylogenetic diversity pattern: 99%, –0.0007653*; 97%, –0.0004603*; 94%, –0.0002757*; 90%, –0.0001679. Asterisks indicate that the decrease in diversity with elevation is significant ($P < 0.05$) based on linear regression analysis.

the angiosperm phylogenic tree topology was constructed by using the widely accepted supertree approach (Webb and Donoghue, 2005), and branch lengths were assigned based on estimates of the minimum age of internal nodes (see *Materials and Methods*). Comparative analyses using molecular approaches alone for both plants and microbes would improve our confidence in such phylogenetic comparisons. Such approaches will be facilitated in the future by increased accessibility to molecular data.

Microorganisms (especially prokaryotes) are very diverse in soils (Torsvik *et al.*, 1990; Janssen, 2006). On par with most microbial diversity studies, it is likely that we sampled the most abundant taxa in each soil core along the elevational gradient. Sampling effort (i.e., the proportion of a community that is sampled) is known to significantly influence taxonomic biodiversity patterns (Plotkin *et al.*, 2002; Woodcock *et al.*, 2006; Green and Plotkin, 2007; Morlon *et al.*, 2008). To our knowledge the influence of sampling effort on phylogenetic biodiversity patterns has not been explored. For example, estimators are available to predict the taxon richness (Hughes *et al.*, 2001) and taxon similarity (Chao *et al.*,

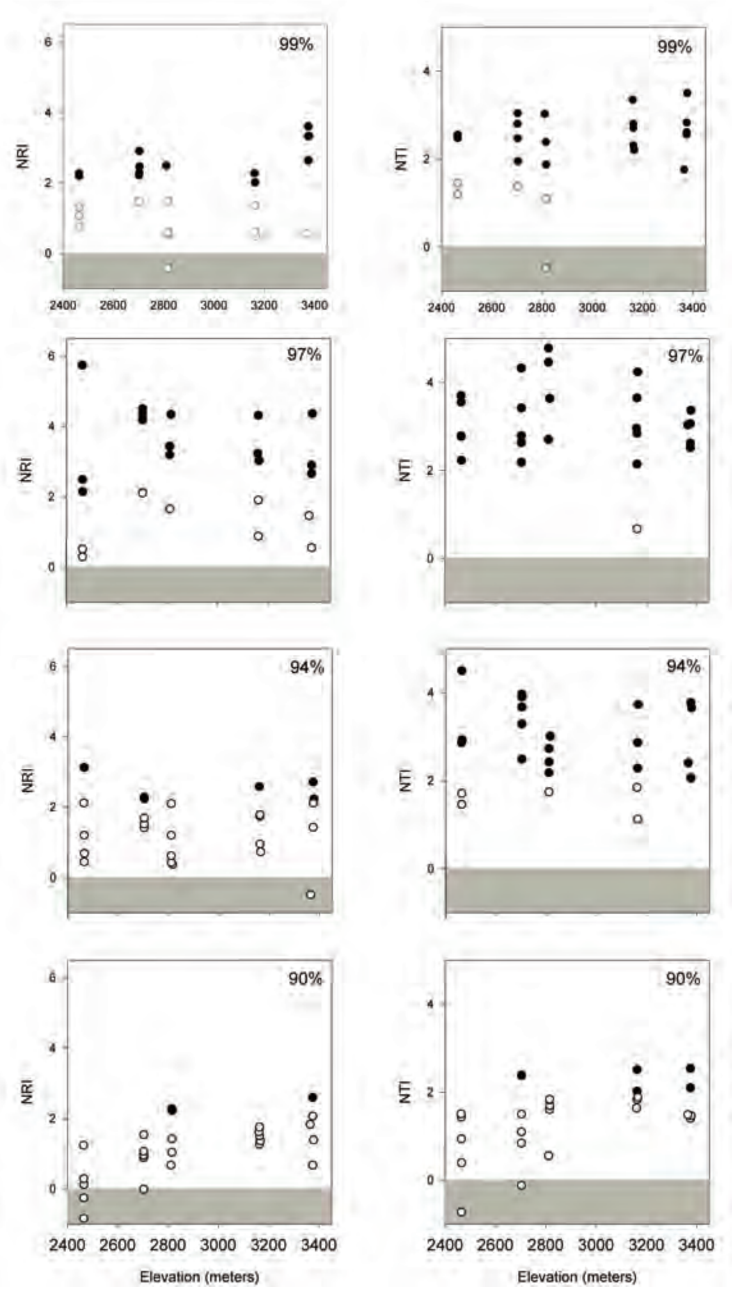

FIGURE 7.5 Microbial NRI and NTI values across the elevational gradient at four different taxonomic resolutions. Observed community phylogenetic structures unlikely to arise by chance ($P < 0.05$) are depicted with solid circles.

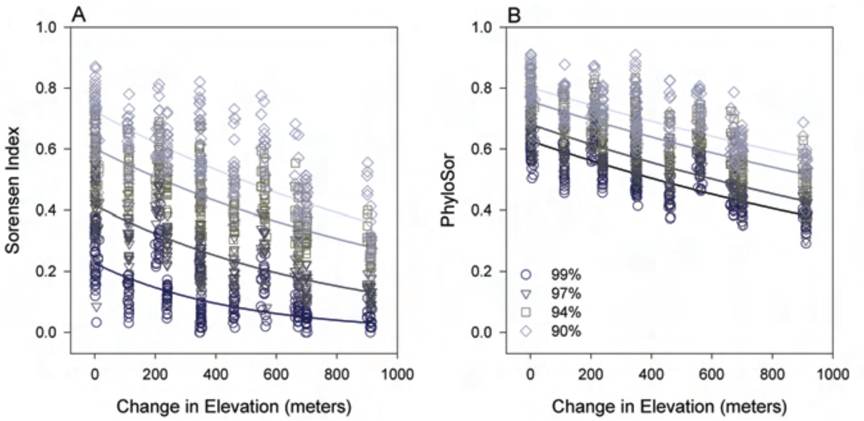

FIGURE 7.6 (*A*) Compositional and (*B*) phylogenetic similarity of *Acidobacteria* communities at four taxonomic resolutions. The compositional and phylogenetic similarity between *Acidobacteria* communities significantly decreases with increasing elevational separation (Mantel test, $P < 0.001$) at all taxonomic resolutions presented. The slope of the decay of phylogenetic similarity between *Acidobacteria* communities is significantly steeper than predicted by a null model constrained by the decrease in taxon similarity ($P < 0.05$). As in Figure 7.3, lines represent an exponential model fit to the observed data.

2005) of ecological communities from sample data, but there are currently no estimators to predict phylogenetic richness, phylogenetic structure, or phylogenetic turnover from sample data. A new generation of estimators is needed for future comprehensive studies that examine taxonomic and phylogenetic diversity patterns in parallel.

As discussed by others, a promising approach to understanding elevational diversity patterns (Rahbek, 2005), and more generally biodiversity patterns (Green and Bohannan, 2006), is to conduct intertaxonomic comparisons to elucidate the spatial and taxonomic scales and degree of sampling effort over which microbial biodiversity relationships approach those of macroorganisms. Such an approach is ambitious, but increasingly tractable as molecular approaches advance our ability to comprehensively characterize biodiversity. Here, we have shown that across an elevation gradient, plant and microbial communities exhibit different patterns of diversity. Phylogenetic-based analyses suggest that the evolutionary and ecological processes driving the biogeographic patterns may differ significantly between these two domains of life. Further work is needed to link the phylogenetic patterns to functional differences among plant and bacterial taxa. Such comparative analyses are needed to provide the empirical foundation for a truly inclusive and predictive theory linking patterns of biodiversity to ecosystem function.

MATERIALS AND METHODS

Study Site and Sampling

We sampled angiosperm and *Acidobacteria* communities at five sites along an elevational transect located near the Rocky Mountain Biological Laboratory, Gunnison County, Colorado. The sites extend from 2,460 to 3,380 m above sea level and spanned a geographic distance of 39 km. Within each study site, we placed five 1-m by 1-m quadrats in a subtransect running down the slope. Three soil samples, separated by 1 cm, were collected adjacent to the middle, highest, and lowest quadrats at each site (nine total). All soil samples were collected from the B-horizon by using sterile glass collection jars. After collection, the soil samples were homogenized and stored at –80°C until analysis.

Average soil temperature at each site was measured by placing Hobo Temperature Data Loggers (OnSet) at 10-cm depth in relatively open patches and recording soil temperature every hour for the month of July in 2007. Total carbon and nitrogen in the soil samples were measured by using a Costech ECS 4010 CHNS-O system. Soil pH was measured after shaking a soil water (1:3 wt/vol) suspension for 30 min. Soil moisture was measured gravimetrically. ArcGIS data and area photos were used to calculate slope and aspect of the sites. These data had a 15.24-cm resolution per pixel and a horizontal accuracy of 60–90 cm.

Characterization of *Acidobacteria* Communities with 16S Clone Libraries

At each site, the bacterial communities within the three soil samples collected adjacent to the middle quadrat and one soil sample adjacent to the lower and upper quadrats were characterized by using sequence analysis of clone libraries (five total). DNA was extracted by using Mobio Power Soil DNA Isolation kits (MoBio Laboratories). Triplicate PCRs were carried out on each soil extraction by using the *Acidobacteria*-specific PCR primer set Acid31/Eub518 (Barns *et al.*, 1999). The 25-µl PCR mixtures were composed of 10 µl of 5 Prime MasterMix (5 Prime, Inc.), 14 µl of water, 1 µmol of each primer, and 1 µl of DNA extract. The PCR conditions used were as follows: 3 min at 94°C, 25 cycles of 30 s at 94°C, 30 s at 50°C (Fierer *et al.*, 2005b), 60 s at 72°C, and a final extension for 5 min at 72°C.

Triplicate PCRs were pooled and then gel-purified by using a MinElute PCR Purification kit (Qiagen). Amplicons were ligated into pCR4-

TOPO vectors and cloned by using a TOPO-TA cloning kit (Invitrogen). Ninety-six clones from each soil sample were selected for sequencing. Plasmid purification and sequencing of cloned PCR products was done at the Qiagen Genomic Services/Sequencing facility with an ABI 377 or 377xl sequencer (Applied Biosystems).

A total of 2,239 cloned 16s sequences were aligned with the NAST alignment tool (DeSantis *et al.*, 2006b), and the alignments were manually edited based on conserved primary sequence and secondary structure information in the ARB software package (Ludwig *et al.*, 2004). The phylum affiliation of each sequence was checked by using the BLAST tool within the National Center for Biotechology Information (Altschul *et al.*, 1990). Potentially chimeric sequences were identified by using the Bellerophon server (Huber *et al.*, 2004). Putative chimeric sequences were manually assessed by building trees in ARB that contained a set of reference sequences obtained from the Greengenes database (DeSantis *et al.*, 2006a) and the 5′ and 3′ sides of the putative chimeras. Sequences were removed from the analysis that had 5′ and 3′ ends affiliating with different groups of reference sequences in the tree (Horner-Devine *et al.*, 2004a).

There is no standard definition of microbial species. Therefore we grouped our 2,196 nonchimeric *Acidobacteria* sequences into phylotypes with a <99% sequence similarity cutoff by using the programs PHYLIP (Felsenstein, 1989) and DOTUR (Schloss and Handelsman, 2005). This is a commonly used phylotype designation (Kroes *et al.*, 1999), which provides high phylogenetic resolution. One sequence was randomly chosen to represent each phylotype. The representative sequences were used to build a phylogenetic tree by maximum-likelihood methods using the program phyML (Guindon and Gascuel, 2003).We used Jukes–Cantor and gamma substitution models where the gamma distribution parameter was estimated from the data. Only informative base positions were used to bin sequences into phylotypes and build the microbial phylogenetic tree. All diversity analyses were later repeated by using 97%, 94%, and 90% sequence similarity cutoffs (Figs. 7.4–7.6).

Characterization of Plant Communities

Angiosperms within each quadrat were identified to species level and checked against Rocky Mountain Biological Laboratory (RMBL) Herbarium specimens jointly by B.J.E., A.J.K., and C.L. Vouchers are being prepared for deposition in the RMBL Herbarium and the University of Arizona Herbarium. All plants were identified in 2005, except for the plants at the lowest site, which were sampled in 2006. Plots were sampled near the peak of the growing season, and thus some individuals with later phenologies could not be identified to species. We staggered the plant sampling dates with the aim of sampling each community at the same relative phenological time point. Any individuals that could not be identified to species or differentiated from known species were excluded from the analysis. This affected between 10% and 15% of the possible species at each site. We used version R20031202 of Phylomatic to construct a tree topology consisting of all of the angiosperms identified in all our quadrats, based on the Angiosperm Phylogeny Group (APG) II backbone (Angiosperm Phylogeny Group II, 2003; Webb and Donoghue, 2005) and used results from recent plant cladistics studies to resolve polytomies (Worberg *et al.*, 2007; Winkworth *et al.*, 2008). The final tree we used for our analyses was almost completely resolved to the family level. We assigned branch lengths to the tree by using the Phylocom module BLADJ to constrain the internal nodes with available age estimates (Wikstrom *et al.*, 2001) and interpolated the other nodes for which direct age estimates are not available.

Diversity Analyses

Taxon Richness and Phylogenetic Diversity

We define the term community as all phylotypes originating from a single soil core (bacteria) or species identified in a single quadrat (plants). Taxon richness within each community was quantified as the total number of species or phylotypes within that community. Phylogenetic diversity within each community was quantified as the minimum total branch length connecting all species within the community to the root of the phylogenetic tree (Faith, 1992b). Phylogenetic diversity was calculated by using the pd module within Phylocom-3.40 (by C. O. Webb, D. D. Ackerly, and S. W. Kemble; available at http://phylodiversity.net/phylocom/). We used a rarefaction sampling approach to account for the unequal sample sizes of each microbial community (number of clones) by calculating the mean of the taxon richness and phylogenetic diversity of 1,000 randomized subsamples of each community. Each community was subsampled by the number of clones in the smallest library (75 clones).

Phylogenetic Community Structure

Using the classical NRI and NTI (Webb, 2000; Webb *et al.*, 2002), we measured the extent to which co-occurring species in a community are phylogenetically related compared with what is expected by chance. With both indices, the phylogenetic structure of the observed community was compared to a null expectation obtained by randomly sampling the pool of all of the species identified in the study 1,000 times, while constraining both the number of taxa in the community and species occurrence across communities (Kembel and Hubbell, 2006). Observed values smaller or larger than 975 of the randomizations were considered significantly structured ($P < 0.05$).

Compositional and Phylogenetic Similarity

Compositional similarity between all pairwise comparisons of communities was quantified with the Sørensen Index:

$$\mathrm{Sor}_{ij} = \frac{S_{ij}}{(S_i + S_j)\frac{1}{2}},$$

where S_{ij} is the number of taxa common to both communities i and j, and S_i and S_j are the total number of species found in community i and j, respectively (Krebs, 1998). By analogy, phylogenetic similarity between two communities was quantified by using an index, coined PhyloSor:

$$\mathrm{PhyloSor}_{ij} = \frac{BL_{ij}}{(BL_i + BL_j)\frac{1}{2}}.$$

Here, BL_{ij} is the branch length common to both communities i and j, and BL_i and BL_j are the total branch lengths of community i and j, respectively.

The PhyloSor index ranges from indefinably close to 0 (two communities only share a very small root) to 1 (both communities are composed of the same taxa). Similar approaches have been carried out by Lozupone and Knight (2005) and Ferrier *et al.* (2007) when considering the closely related Jaccard and Bray-Curtis similarity indices. Using PhyloSor, one can test whether two communities are phylogenetically more or less similar than what is expected given their taxa similarity. This is done by comparing the phylogenetic similarity of the observed communities to a null expectation obtained by randomly sampling the pool of all of the species identified in the study while constraining the number of taxa in each community and the number of taxa shared by the two communities.

By analogy with the well-established distance–decay relationship, which describes the decrease in compositional similarity between two communities with increasing geographic distance (or equivalently elevational separation) between them (Soininen *et al.*, 2007), we used PhyloSor to quantify the decrease in phylogenetic similarity with distance (phylogenetic distance–decay). We tested whether the slope in the decay of phylogenetic similarity was greater or less than what was expected given the taxonomic decay in similarity by comparing the observed slope with a distribution of distance–decay slopes obtained by randomizing the location of taxa at the tips of the community phylogenetic tree 1,000 times. This is equivalent to randomly sampling the taxa while constraining the number of taxa in each community, the number of taxa shared by any two communities, and taxa occurrence across all communities. The observed phylogenetic slope was assumed significantly different from the null if it was greater than or less than 975 of the slopes of the randomizations (two-tailed test, $P < 0.05$). To address the unequal sampling of microbial communities, we repeatedly calculated and tested the significance of distance–decay slope on subsampled communities, where communities were subsampled by the number of clones in the smallest library. The significance of results did not differ between repeated subsamples.

Linking Diversity Measurements to Environmental Parameters

To determine the correlation between elevation and potential environmental drivers with the observed diversity patterns, we used polynomial regression analysis. For each environmental variable, we fit a linear and a quadratic regression model. The best model was determined based on Akaikes Information Criterion differences (Burnham and Anderson, 2002). Using a stepwise regression to select variables and interactions, a multivariate model was constructed for each alpha diversity measurement.

Mantel tests (999 permutations) were used to determine whether compositional and phylogenetic similarity decayed significantly with elevational distance (Legendre and Legendre, 1998). Similarity values between pairwise comparisons of microbial communities were the averages of 1,000 rarefaction samples, as described above. The best fit and the most homoscedastic residuals were found in models that used the log transformation of similarity against elevational distance, with the exception of angiosperm taxa similarity, which was best described by a linear–linear distance–decay model. We used Mantel tests to examine correlations between community similarity and environmental similarity [for a discussion of these methods, see Legendre *et al.* (2005) and Toumisto and Ruokolainen (2006)]. We chose the combination of environmental variables that best explained the changes in angiosperm and *Acidobacteria* community composition between samples with BIO-ENV (Clark and Ainsworth, 1993) and tested the importance of these variables after controlling for geographic distance and vice versa by using partial Mantel tests. For all analyses, moisture, carbon, and nitrogen were arcsin(sqrt(y))-transformed and aspect was $1/y$-transformed (Legendre and Legendre, 1998).

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8

Resistance, Resilience, and Redundancy in Microbial Communities

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Although it is generally accepted that plant community composition is key for predicting rates of ecosystem processes in the face of global change, microbial community composition is often ignored in ecosystem modeling. To address this issue, we review recent experiments and assess whether microbial community composition is resistant, resilient, or functionally redundant in response to four different disturbances. We find that the composition of most microbial groups is sensitive and not immediately resilient to disturbance, regardless of taxonomic breadth of the group or the type of disturbance. Other studies demonstrate that changes in composition are often associated with changes in ecosystem process rates. Thus, changes in microbial communities due to disturbance may directly affect ecosystem processes. Based on these relationships, we propose a simple framework to incorporate microbial community composition into ecosystem process models. We conclude that this effort would benefit from more empirical data on the links among microbial phylogeny, physiological traits, and disturbance responses. These relationships will determine how readily microbial community composition can be used to predict the responses of ecosystem processes to global change.

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Recent rates of plant and animal species' extinctions have spurred ecologists to consider the consequences of biodiversity loss. Beyond the ethical and aesthetic reasons for conserving it, biodiversity supplies economically valuable ecosystem goods and services on which human society depends (Ehrlich and Ehrlich, 1992; Daily, 1997). Although most biodiversity and conservation research has focused on the value and importance of large organisms, the sheer abundance of microorganisms confers on them a principal role in providing ecosystem services, such as water purification and soil fertility. Bacteria and Archaea alone contain most of the total nitrogen (N) and phosphorus (P) and up to half of the carbon (C) stored in living organisms (Whitman *et al.*, 1998), and the metabolic machinery of microorganisms drives a variety of ecosystem processes. Indeed, microbes carry out the bulk of decomposition and catalyze important transformations in the C, N, sulfur, and P cycles.

Despite their importance to the functioning of ecosystems, microorganisms are rarely explicitly considered in individual ecosystem or global process models. In addition to methodological hurdles, a primary reason for this gap is their overwhelming diversity. Estimates of soil microbial diversity range from thousands to a million microbial "species" in a few grams of soil (Torsvik and Øvreås, 2002; Gans *et al.*, 2005), and how this diversity is related to ecosystem processes is generally unknown (Torsvik *et al.*, 2002; Crawford *et al.*, 2005; Azam and Malfatti, 2007). Moreover, it is infeasible to assess and track each microbial taxon in an ecosystem, let alone include even a small fraction of these taxa in ecosystem models.

Because of these obstacles, ecosystem models often "black box" microbiology. In other words, microorganisms are buried within equation structure as kinetic constants and response functions and are "simplified beyond recognition" (Schimel, 2001). As a result, the abundance, diversity, and interactions of microorganisms are often assumed to be unimportant to ecosystem processes, particularly in terrestrial ecosystem models. [A number of ocean ecosystem models include various phytoplankton groups (e.g., Moore *et al.*, 2002; Salihoglu and Hofmann, 2007)].

In contrast to microorganisms, it is generally accepted that plant biodiversity (both richness and composition) affects terrestrial ecosystem processes (Tilman *et al.*, 1997; Hector *et al.*, 1999; Spehn *et al.*, 2005) and influences ecosystem responses to disturbances such as CO_2 and N addition [e.g., Reich *et al.* (2001)]. Plant community composition is often incorporated into large-scale models through the use of functional groups, which are based on plant traits (Tilman *et al.*, 1997; Reich *et al.*, 2007). Global change models—whether of ecosystems (Haxeltine and Prentice, 1996; Moorcroft *et al.*, 2001), the terrestrial biosphere (Foley *et al.*, 1996), or global climate (Cox *et al.*, 2000; Higgins and Schneider, 2005)—routinely incorporate 5–10 plant functional groups to improve model predictions.

Nonetheless, researchers are calling for a better understanding of the functional traits of plant species to help predict ecosystem processes under changing environmental conditions (Diaz *et al.*, 2004; Arndt, 2006; McGill *et al.*, 2006).

Given the central role of microbes in ecosystem processes, we contend that microbial composition might be at least as important as plant composition for building predictive ecosystem models. Here we discuss two major hurdles to including microorganisms in ecosystem models. The first is a general idea that microbial composition does not matter to ecosystem processes. The second is that microbial composition may be too diverse to model. To address the first hurdle, we outline three conditions that would need to be true for changes in microbial composition to matter to ecosystem processes. We then review recent studies to assess whether particular microbial groups may be more or less subject to particular disturbances. We address the second hurdle by proposing a simple model of microbial process rates that incorporates information on community composition. The model is used to illustrate how empirical data could be used to predict microbial process rates under disturbance, even for relatively diverse communities. Because it is not feasible to add a parameter for each microbial population in a community, we consider when coarse information about microbial composition, such as the relative abundance of a few key clades within a functional group, could help decrease uncertainty about predictions of ecosystem processes.

A FRAMEWORK WITHIN THE BLACK BOX

Schimel (2001) points out that black box ecosystem models make two implicit assumptions: that microbial processes can be represented across a range of environmental conditions with one mathematical function, and that microbial processes are never limited by the abundance of any microorganism. These assumptions are implicit because no major ecosystem models include parameters that explicitly represent components of microbial community composition. At best, some models include total microbial biomass as a parameter [e.g., Harte and Kinzig (1993)], but many widely used models such as CENTURY (Parton *et al.*, 1987), MEL (multiple element limitation) (Rastetter *et al.*, 1997), and TEM (terrestrial ecosystem model) (McGuire *et al.*, 1993) contain parameters related to microbial processes but not the microbial communities themselves. Ocean biogeochemistry models have only just begun to incorporate explicit parameters that capture plankton community composition (Moore *et al.*, 2002; Le Quéré *et al.*, 2005; Salihoglu and Hofmann, 2007).

These models implicitly assume that changes in community composition will not affect ecosystem processes, because there is no mechanism for such changes to influence model predictions. This assumption may be valid if microbial composition is resistant, resilient, and/or functionally redundant (these terms and others are defined in Table 8.1). Microbial composition is resistant if it is similar across a variety of environmental conditions—in other words, it is difficult to perturb from an original state. It is resilient if, when composition does change, it recovers quickly, whether by growth or by physiological or genetic adaptation. Finally, microbial composition may change in response to new environmental conditions but contain functionally redundant taxa such that ecosystem process rates are not altered. If these conditions are not generally true for microbial communities, then many current ecosystem models may fail at predicting the rates of microbe-driven processes under disturbance.

The idea that microorganisms are resistant, resilient, and functionally redundant is pervasive in ecology. Some microbial groups show a high degree of metabolic flexibility and physiological tolerance to changing environmental conditions [e.g., Meyer *et al.* (2004)], which could result in microbial communities that are resistant to change. These traits and others associated with microbes—such as high abundances, widespread dispersal, and the potential for rapid growth rates—have also led to the suggestion that microbial communities will be resilient to change (Fenchel and

TABLE 8.1 Summary of Definitions Used in This Chapter

Term	Definition
Functional group	All organisms that directly contribute to the rate of a particular functional process in an ecosystem
Functional redundancy	The ability of one microbial taxon to carry out a process at the same rate as another under the same environmental conditions
Functional similarity	The ability of two microbial communities to carry out a functional process at a similar rate, regardless of differences in composition
Microbial composition	The richness, relative abundance, and phylogenetic structure of taxa in an assemblage
Microbial taxon	A group of phylogenetically related microbes
Resilience	The rate at which microbial composition returns to its original composition after being disturbed
Resistance	The degree to which microbial composition remains unchanged in the face of a disturbance
Physiological trait	A physiological characteristic that determines the contribution of a microbial taxon to a functional process
Physiological response curve	The function describing the relationship between the process contribution of a microbial taxon and disturbance intensity

Finlay, 2004; Meyer, 1994). Furthermore, rapid evolutionary adaptation through horizontal gene transfer could allow sensitive microorganisms to adapt to new environmental conditions and quickly return the community to its original composition. The extremely high abundance and diversity of microorganisms are used as an argument for functional redundancy, because it is difficult to imagine that biogeochemical cycling is limited by microbial abundance (Meyer, 1994) or genetic diversity (Finlay *et al.*, 1997).

Fig. 8.1 illustrates the potential impacts of a disturbance on microbial composition and/or ecosystem processes. Consider a disturbance applied to an ecosystem and the microbial communities within it. Microbial composition might be resistant to the disturbance, and not change. Alternatively, if the community is sensitive and does change, it could be resilient and quickly recover to its initial composition. Finally, a community whose

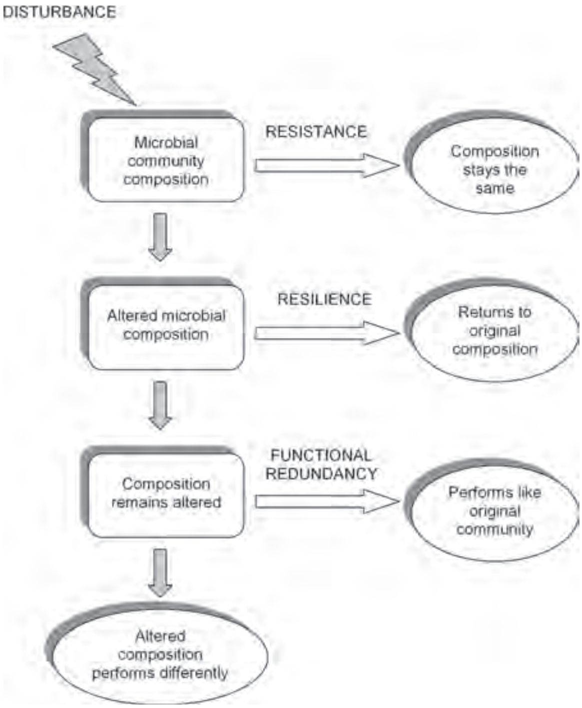

FIGURE 8.1 A schematic of how disturbance can change microbial composition and thereby affect ecosystem processes versus when disturbance would not have this effect (when the microbial community is resistant, resilient, or functionally redundant).

composition is sensitive and not resilient might produce process rates similar to the original community if the members of the community are functionally redundant.

Only if community composition is sensitive to a disturbance, not resilient, and functionally dissimilar to the original community do changes in community composition matter for predicting ecosystem process rates. In addition, the degree to which a community is resistant, resilient, and functionally similar will influence the degree to which community composition matters to a particular process. For instance, even if microbial composition is highly sensitive and not resilient to a disturbance, if all of the taxa perform a process at very similar rates (that is, they are nearly functionally redundant), then predictions of ecosystem process rates will not be improved much by including information about microbial composition.

This conceptual framework does not exclude the possibility that there is little change in microbial composition but large changes in ecosystem process rates. This scenario would suggest that the changes are a direct effect of environmental changes, the result of compositional changes in other organisms such as plants, or immediate physiological responses of microorganisms that are not accompanied by compositional changes. An example of the latter is that some transformations such as decomposition occur faster at higher temperatures. This is seen immediately, before changes in composition could be responsible (Fierer *et al.*, 2005a).

RESISTANCE OF MICROBIAL COMPOSITION

To assess whether microbial composition is often resistant to disturbance, we reviewed studies that experimentally exposed microbial communities to various disturbances. We searched Web of Science for papers including "microb*" and "community composition" in their titles, abstract, or subject words. In addition, we specifically searched the journal *Global Change Biology* for global change experiments that assessed microbial composition. We did not limit papers by study system, but the majority of studies returned by these search parameters focused on terrestrial soils. We acknowledge that there are many manipulative marine studies that we did not pick up in our search. The disturbances we examined were limited to CO_2 enrichment, temperature, fertilization with mineral nutrients, and enrichment with C substrates (including complex organics such as manure and potential toxins such as pesticides). We reason that these four disturbances are typical of those that ecosystems experience under human-driven global change. Finally, we did not intend the literature search to be exhaustive, but to be representative of these types of studies.

We hypothesized that differences in focus and methodologies among the studies would influence the likelihood of detecting a compositional response. Therefore, for each study we recorded the breadth of the taxonomic group targeted (e.g., bacteria and fungi; methanotrophic bacteria), the habitat, the method used to examine composition, and the disturbance applied, as well as whether composition of the target group changed in response to the disturbance. We also recorded the time after the disturbance was first applied at which composition was assessed, which is relevant for the discussion of resilience below.

Papers from this search included studies that targeted composition broadly such as with phospholipid fatty acid analysis, which targets bacteria and fungi. In contrast, other studies examine narrower functional guilds within the Bacteria by PCR-amplifying a functional gene followed by a fingerprinting technique (such as denaturing gradient gel electrophoresis or terminal restriction fragment length polymorphism). Thus, the breadth of the taxa studied varied widely and is related to the methodology used to evaluate community composition. The methodology itself might also have an influence on whether a change in composition is detected. For instance, sequencing of PCR-amplified clone libraries will reveal finer-scale genetic changes than fingerprinting methods that target the same gene. Finally, because we were interested in compositional changes, our search excluded many studies that measure only total microbial biomass [e.g., those reviewed in Wardle (1992)].

Table 8.2 summarizes the results by the four disturbance types. The majority of these studies demonstrate that composition is sensitive to disturbance. More than 80% of the mineral fertilization (N/P/K), temperature, and C amendment studies found significant effects of disturbance on microbial composition. In contrast, the effect of elevated CO_2 was found less often, in only 60% of the studies.

TABLE 8.2 Summary of Studies, Including the Percentage of Studies in Which Microbial Community Composition Was Sensitive to the Disturbance, and the Average Length of Studies That Found Resistant Versus Sensitive Composition

Disturbance	No. of Studies	Percentage of Studies Sensitive	Average Length of Study (years ± SD)		
			Resistant	Sensitive	*P* value
CO_2 increase	20	60	3.3 ± 1.9	3.6 ± 1.9	0.78
N/P/K fertilization	38	84	4.8 ± 4.5	8.2 ± 8.7	0.17
Temperature	11	82	1.1 ± 1.3	3.0 ± 5.0	0.35
C amendments	41	83	0.15 ± 0.09	4.9 ± 12.6	0.03

NOTE: The *P* value reported is the result of a *t* test (assuming unequal variances) between the study times for the resistant versus sensitive studies.

These studies did not suggest that broad taxonomic groups are more or less sensitive to disturbances than narrow taxonomic groups. This pattern suggests that taxonomic breadth is not related to whether a compositional shift was detected. Perhaps more surprisingly, there are no patterns suggesting that methodology influences whether a compositional change was detected. In addition, we were not able to discern whether particular taxonomic or functional groups are more or less sensitive to particular disturbance types. Overall, the low number of studies observing a resistant microbial composition hinders our ability to recognize any patterns among these studies. However, we can conclude that microbial composition is generally sensitive to disturbance.

RESILIENCE OF MICROBIAL COMPOSITION

Even if microbial composition is sensitive to a disturbance, the community might still be resilient and quickly return to its predisturbance composition. A number of features of microorganisms, and in particular Bacteria and Archaea, suggest that resilience could be common. First, many microorganisms have fast growth rates; thus, if their abundance is suppressed by a disturbance, they have the potential to recover quickly. Second, many microbes have a high degree of physiological flexibility. This is famously the case for the purple nonsulfur bacteria, which can be phototrophs under anoxic conditions and heterotrophs under aerobic conditions. Thus, even if the relative abundance of some taxa decreased initially, these taxa might physiologically acclimate to the new abiotic conditions over time and return to their original abundance. Finally, if physiological adaptation is not possible, then the rapid evolution (through mutations or horizontal gene exchange) could allow microbial taxa to adapt to new environmental conditions and recover from disturbance. All of these arguments assume that abundance is reduced by a disturbance, but some microbial taxa may benefit from the new conditions and increase in abundance. Thus, in order for some taxa to recover in abundance, those that responded positively to the disturbance would also need to decrease in abundance to return the community to its original composition.

Few studies explicitly focus on the time course of microbial composition after a disturbance; instead, most focus solely on the sensitivity of composition. Consequently, we recorded the length of time between the application of the disturbance and when microbial composition was assessed for the studies in our sample. If composition is highly resilient, then one should be less likely to detect a compositional change as time from disturbance increases.

We compared the time from initial disturbance for those studies that found composition to be sensitive versus resistant. Generally, the timing of compositional assessment varied widely, from just a few hours to decades. For C amendments, the studies in which microbial community composition changed were significantly longer than studies that did not detect a change (Table 8.2). This result implies that there is a lag in the response of microbial communities to C additions and does not support the idea that these communities are resilient. For elevated CO_2, mineral fertilization, and temperature, all studies were equally likely to find shifts in community composition, regardless of time since disturbance. On average, the reviewed studies examined composition after several years of the disturbance application. Thus, as a conservative boundary, microbial composition is often not resilient within a few years.

Certainly, the strength of the disturbance and how often it is applied will have an effect on the resilience of microbial composition. Most of the studies we reviewed continued to apply the disturbance throughout the study (as occurs for most global change disturbances), rather than a one-time application at the beginning of the experiment. For instance, Enwall *et al.* (2007) compared fertilized and unfertilized soil plots that have been maintained since 1956. The composition of the general bacteria and ammonia-oxidizing bacteria still differs between the plot types. In contrast, Stark *et al.* (2007) applied organic and inorganic forms of N to soil samples and compared the composition of Actinomycetes, alpha-Proteobacteria, and Pseudomonads. After 10 days, composition differed between the soil treatments, but after 91 days composition differed only among the Pseudomonads. Conversely, some of the studies that found no effect of disturbance on composition might have found an effect if the study was carried out longer.

FUNCTIONAL REDUNDANCY OF MICROBIAL COMPOSITION

Our literature survey clearly indicates that microbial communities are sensitive to disturbance and often do not rapidly recover to their original state. These responses beg the question of whether compositional shifts will affect ecosystem processes—will the disturbed community be functionally similar to the original community? There are two reasons why changes in microbial composition might not affect ecosystem process rates. First, the new community might contain taxa that are functionally redundant with the taxa in the old community. Second, taxa in the new community may function differently but result in the same process rate when combined at the community level.

What do we know about functional redundancy in microbial communities? Few studies compare the degree of redundancy within different microbial functional groups [but see, for example, Wohl *et al.* (2004) and Setälä and McLean (2004)]. Functional redundancy is difficult to establish because it requires detailed knowledge about the microbial populations that perform a specific process. Furthermore, organisms that are functionally redundant under one set of conditions may not be under different conditions. In general, we know little about the distribution of functional traits across microbial taxa despite years of recognition of this need (Schimel, 2001).

Nonetheless, a growing body of literature has begun to address the more basic question of whether microbial composition matters to ecosystem processes to any degree versus whether the members of a functional group are completely redundant. To address this question, one needs to manipulate microbial composition while controlling for the abiotic environment. This is because any differences in process rates can then be attributed directly to compositional differences and not simply to physiological responses of the original community under new environmental conditions. In plant communities, composition and diversity can be manipulated directly by sowing and weeding plots in the field. Although this is not an easy task, it is much more feasible than manipulating microbial community composition in the field.

A number of approaches can be used to disentangle compositional versus environmental effects on ecosystem processes. In one approach, process rates are measured before and after a disturbance manipulation but before microbial composition changes. This measurement gives some idea about the direct effect of the disturbance on process rates independent of community composition. Schimel and Gulledge (1998) review studies that subject microbial communities from different habitats to parallel short-term, environmental treatments and compare the communities' process rates. For instance, Gulledge *et al.* (1997) found that rates of methane consumption by methanotroph communities in response to ammonium fertilization varied depending on whether the communities were associated with paper birch or white spruce taiga forests. This result suggests that differences in methanotroph composition are responsible for differences in the physiological responses.

Although they may not mimic natural communities, bioreactors are useful model systems for linking microbial functional groups with process rates. Community composition can be manipulated directly to test the functional contribution of different microbial taxa. In addition, the communities can be perturbed and monitored for function and composition over time. For example, Fernandez *et al.* (2000) constructed two different methanogenic bioreactor communities that functioned similarly before disturbance with a glucose pulse. After the pulse, the communities metabolized glucose using different pathways and regained prepulse function at different rates. The authors were able to attribute these differences to specific groups of bacteria that showed different metabolic functions.

Transplant experiments can also be used to separate environmental versus compositional effects on process rates (Reed and Martiny, 2007). If different microbial communities produce different process rates in a common environment, then it can be inferred that the compositional differences are responsible for the functional differences. Balser and Firestone (2005) provide a good example of how the transplant approach can also be used to make linkages between microbial taxa and process rates under disturbance. They transplanted soil microbial communities across a climate gradient and demonstrated that community composition affected process rates independent of climate. Furthermore, they used phospholipid fatty acid data to correlate process rates with specific members of the microbial community and concluded that nitrification potential and N_2O flux were likely driven by Gram-negative bacteria.

Although not often possible, direct manipulations of microbial composition can provide useful information about the functional status of microbial groups, especially when coupled with process rate measurements. For example, specific taxa can be targeted for elimination from a community via chemical or physical means and process rates compared in communities with and without the taxa (Santos and Whitford, 1981; Griffiths *et al.*, 2000; Austin *et al.*, 2006). Wertz *et al.* (2007) manipulated soil microbial composition by serial dilution and reinnoculation of sterile microcosms; they found no effect of composition on functioning in the microcosms. Alternatively, communities can be artificially constructed to contain specific taxa and to establish links between composition and process rates (Naeem *et al.*, 2000). For instance, Bell *et al.* (2005) showed that the diversity and composition of bacteria influenced respiration rates in aquatic microcosms.

The literature reviewed in the sections above suggests that microbial composition is often altered by disturbances and does not recover over some time. Furthermore, these changes often impact the rates of ecosystem processes, suggesting that at least some microbial taxa are functionally dissimilar. In light of these observations, we propose a broad framework in the next section for integrating information about microbial composition into predictive models of ecosystem processes.

INCORPORATING MICROBES INTO MODELS: PHYSIOLOGICAL TRAITS AND PROCESS RESPONSE CURVES

As more data are collected on the relationship between microbial composition and ecosystem functioning, explicitly incorporating microbes into process models will become increasingly tractable. Indeed, analogous efforts have been successful with plant functional groups and ecosystem models. However, there are some gaps to bridge between microbial ecologists and ecosystem modelers. Modelers are uncertain about how to aggregate extremely diverse microbial communities into a manageable number of functional units. Conversely, microbial ecologists often have a poor understanding of the types of studies that would be useful to modelers in carrying out this aggregation step. In this section we outline a simple microbial process model to frame some of the results above and consider how experimentalists might further inform predictive models.

Consider a number of taxa within a functional group that all contribute to an ecosystem process. The functional group has n taxa with abundances a_i (in units of biomass) and biomass-specific physiological rates r_i. The community process rate R is the sum of the products of the abundances and the rates:

$$R = a_1r_1 + \ldots + a_nr_n.$$

If taxon 1 and taxon 2 have the same physiological rates r_i, then they are functionally redundant, and their abundances can be aggregated together:

$$a_1r_1 + a_2r_2 = (a_1 + a_2)r_1.$$

If communities 1 and 2 have different compositions but the same process rates ($R_1 = R_2$), then we can define these communities as functionally similar, although they may contain taxa that are not functionally redundant.

To predict how microbial processes will respond to disturbance, we also need to know the physiological responses of each taxon to disturbance. Assume that the physiological response curve $r(I)$ is a linear function of disturbance intensity I:

$$r(I) = m \times I + r_0,$$

where m is the slope and r_0 is the physiological rate under undisturbed conditions (Fig. 8.2). For the microbial community as a whole, the process rate as a function of disturbance intensity I would be

$$R(I) = a_1(I)r_1(I) + \ldots + a_n(I)r_n(I).$$

Because it is not feasible to model all taxa and their responses individually, the challenge is to determine properties of the functional group that will help predict the responses of ecosystem processes to disturbance. A worthwhile goal for future experimental studies would be to identify the level of redundancy in physiological traits and disturbance responses within microbial functional groups. Then one could estimate the parameters m

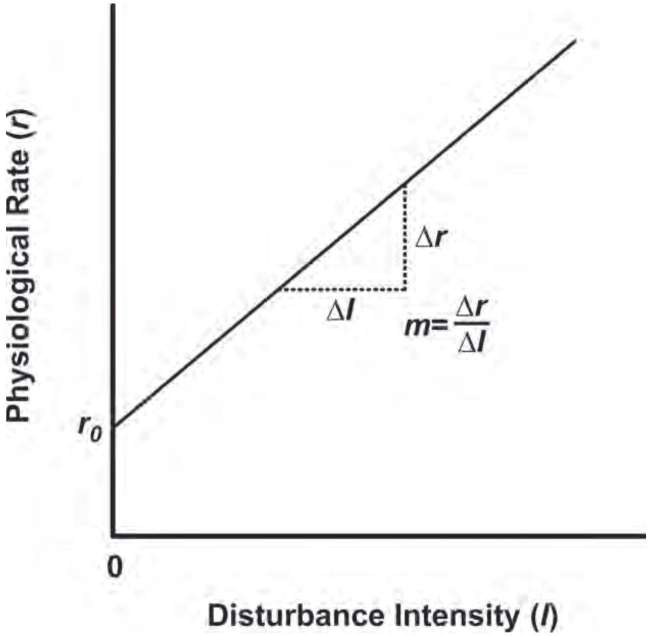

FIGURE 8.2 A physiological response curve for a microbial taxon. The curve illustrates the rate at which the taxon contributes to an ecosystem process as a function of disturbance intensity. For simplicity, this function is assumed to be linear, although other forms are likely for microbial taxa. The slope *m* of the line indicates how quickly the physiological rate changes with *I*, and r_0 is the physiological rate in the absence of disturbance.

and r_0 without having to measure them for every taxon. For example, if there is correspondence between phylogeny and a physiological trait (r_0), or between phylogeny and functional responses (*m*), then we could use phylogenetic information to estimate the parameters. Given that microbial composition is usually assessed with phylogenetic markers, this information could be used to predict how members of a functional group influence ecosystem process rates.

As an illustration of this approach, consider the functional group in Fig. 8.3*A*. All of the taxa in the top clade perform the functional process at a high rate (denoted by the large circles), and those in the bottom clade perform the process at a lower rate (denoted by the small circles). If the total abundance of these two clades stays the same, then shifts in composition within the two clades are not functionally important, as taxa within the clades perform the function at the same rate. In the model more

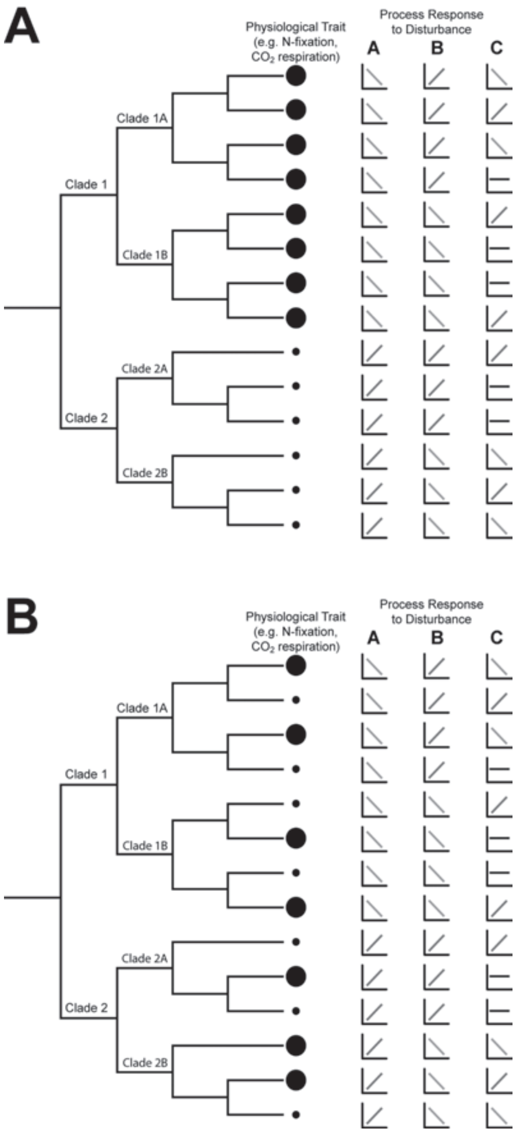

FIGURE 8.3 A stylized illustration comparing the phylogenetic relationship of physiological traits versus process responses to disturbance among taxa. Different rates of the physiological traits are represented by differently sized circles (see text for further explanation). In *A*, physiological trait values are correlated with phylogenetic similarity, whereas in *B*, physiological trait values are randomly distributed among taxa. Three different disturbances (**A**, **B**, and **C**) produce process responses from the taxa that are also either phylogenetically related (disturbances **A** and **B**) or randomly distributed among taxa (disturbance **C**).

generally, these clades define the level of aggregation for an undisturbed community contributing to process *R*, such that

$$R = a_{c1}r_{0c1} + a_{c2}r_{0c2},$$

where a_{c1} and a_{c2} are the summed abundances of all taxa in clades 1 and 2 and r_{0c1} and r_{0c2} are the physiological rates for the taxa in clades 1 and 2, respectively.

As with the physiological trait in Fig. 8.3*A*, the disturbance responses may also be related to phylogeny. For instance, the taxa within clade 1 all respond similarly to disturbance A, as do the taxa within clade 2. Therefore, only the abundances of these two clades must be considered to predict the overall process rate *R* under disturbance:

$$R(I) = a_{c1}(m_{c1} \times I + r_{0c1}) + a_{c2}(m_{c2} \times I + r_{0c2}),$$

where m_{c1} and m_{c2} represent the slopes of the physiological response curves for clades 1 and 2, respectively. We note that the abundances under disturbance must be determined before the calculation of the new process rate unless they are known to be stable with disturbance.

For modeling purposes, it would be useful to know the relationships among physiological rates, disturbance responses, and phylogenetic position among taxa. Then, predictions of process rates could be estimated based on the abundances of relatively broad phylogenetic groups. However, we currently lack the empirical evidence necessary to establish which microbial processes show a strong correspondence between phylogeny and physiology. Although this topic has received much attention in the microbial ecology literature (Andren and Balandreau, 1999; Balser *et al.*, 2002; Nannipieri *et al.*, 2003), few studies have tested the linkage convincingly.

Disturbance B in Fig. 8.3 illustrates a case where the physiological response curves are phylogenetically grouped at the level of subclades (denoted 1A, 1B, 2A, and 2B). In the general model, we would calculate the process rate as

$$\begin{aligned} R(I) = a_{c1A}(m_{c1A} \times I + r_{0c1}) + a_{c1B}(m_{c1B} \times I + r_{0c1}) \\ + a_{c2A}(m_{c2A} \times I + r_{0c2}) + a_{c2B}(m_{c2B} \times I + r_{0c2}). \end{aligned}$$

This model is considerably more complex than the prior model because of the heterogeneity in disturbance responses at the subclade level. In a complex microbial community this situation is likely to occur but is still tractable for modeling if the heterogeneity is relatively low and well characterized. For instance, Horz *et al.* (2005) found that two different clades of methanotrophs responded differently to simulated global change. The worst-case scenario is that the responses of the taxa to disturbance are randomly distributed across the phylogeny as illustrated by disturbance C in Fig. 8.3. In this case, calculation of the overall process rate requires the abundances of each individual taxon. A similar challenge would arise if the functional trait itself is not phylogenetically determined (Fig. 8.3*B*).

One promising set of tools for overcoming the challenges of these "worst-case" scenarios are metagenomic or metatranscriptomic approaches. For example, environmental gene tags (EGTs) could potentially be used as a proxy for physiological rates or disturbance responses across the whole community, even if these traits are unrelated to phylogeny (Tringe *et al.*, 2005). With this technique, the abundances of genes specific to particular environmental processes (such as phosphate metabolism) could be extracted from community metagenomic data and used in modeling process rates. Another advantage of this approach is that multiple EGTs and processes can be examined in a single sample, rather than constructing separate clone libraries for each different functional gene of interest.

In our model, when does changing composition matter to ecosystem processes? Changing the abundance of a taxon will affect the process rate unless the abundances of other taxa also change to compensate. In undisturbed communities, exchanging one taxon for another (with similar biomass) can affect the community process rate if the two groups have different r_0 (physiological rate) values. With disturbance, composition matters if taxa with different m (disturbance response) values change in abundance (even if they had the same r_0 values). Although our simple model considers only the total abundances (i.e., biomasses) of different taxa, we note that changes in body size distributions within or across taxonomic groups could also affect ecosystem process rates as suggested by metabolic scaling theory (Enquist *et al.*, 2003).

In communities with a large number of taxa, a "portfolio effect" may prevent the community process rate from changing with disturbance, even if the taxa change in abundance and are not functionally redundant (Doak *et al.*, 1998). The portfolio effect can occur when positive responses of some taxa are averaged with negative responses of other taxa, resulting in no net change in function. Thus, the greater the number of taxa that perform a process, the more buffered the process is to environmental perturbations (Schimel, 1995). This portfolio mechanism (in addition to functional redundancy) could lead to similarity in community function despite changes in microbial composition.

CONCLUSIONS

There are three ways in which microbial composition might not matter to ecosystem functioning in the face of disturbance. First, microbial communities might be resistant to change. However, we find that microbial composition is, in the majority of cases that we reviewed, sensitive to elevated CO_2, mineral fertilization, temperature changes, and C amendments. Second, microbial composition might be resilient and quickly return to its original state. The literature suggests that, at least over the timescale of a few years, microbial composition usually still differs from that of undisturbed communities. Third, even if microbial composition changes, the new community might be functionally similar to the original. Although this hypothesis is currently difficult to test, recent studies suggest that the taxa in many microbial communities are probably not functionally redundant and different communities are not functionally similar.

How can the information that microbial composition affects ecosystem functioning be used to improve predictions of ecosystem process rates under disturbance? The simple model we presented in the previous section highlights two lacking pieces of information. First, more data are needed on the responses of microbial taxa to disturbance, in addition to knowledge about physiological traits. Microbial taxa may vary in their responses to different disturbances, and these taxa may not correspond to functional groups defined by physiological traits.

Second, it would be useful to know the relationship among microbial phylogeny, physiological traits, and response curves. Although it is clear that phylogenetic relationships of taxa are not perfect predictors of microbial physiology (Achenbach and Coates, 2000; Konstantinidis and Tiedje, 2005), there are phylogenetic signals of physiological traits [e.g., Fierer *et al.*, 2007]. The genetic scale at which these traits are clustered would guide modelers in aggregating microbial taxa for their models. Similarly, we know of no studies that address the relationship between phylogeny and microbial responses to disturbance. For instance, perhaps the response of microbial taxa to particular C amendments are predictable at very fine phylogenetic scales (e.g., >99% 16S rDNA similarity), whereas the responses of taxa to temperature changes can be aggregated at a broader scale (such as at >95% similarity).

In sum, there has been increasing recognition that microbes are relevant to ecosystem processes and enormous progress in characterizing the response of microbial composition to disturbance, particularly in soils. Despite these advances, the field of microbial ecology lacks a strong predictive framework to interpret the functional consequences of changes in microbial composition. Much more empirical work is needed to define microbial functional groups and their responses to various disturbances. Greater efforts toward improving culture techniques and assessing the physiological responses of microbial populations under controlled conditions would be especially useful. Once explicitly incorporated into models, this information could greatly enhance our ability to predict ecosystem responses to global change.

ACKNOWLEDGMENTS

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Part III

TRENDS AND PROCESSES IN THE PALEONTOLOGICAL PAST

Extinction has always been a part of life on Earth and is the ultimate fate of all species. Rates of extinction have varied across time, from standard or “background” rates to occasional mass events. The chapters in this section place the current biodiversity crisis in temporal perspective by scrutinizing the fossil record for patterns and processes of extinction in the distant and near past.

The fossil record traditionally has been interpreted to register five episodes of wholesale biotic change so severe as to qualify as mass extinctions: at the end of the Ordovician (ca. 444 Mya), Devonian (360 Mya), Permian (252 Mya), Triassic (200 Mya), and Cretaceous (66 Mya). Each was characterized (indeed identified) by a substantial loss of then-extant taxa. In Chapter 9, Douglas Erwin reexamines these five mass extinction events in terms of the respective impacts on each of seven metrics of biodiversity—taxonomic diversity, phylogenetic diversity, morphologic disparity, functional diversity, architectural diversity, behavioral complexity, and developmental diversity—which potentially capture different aspects of the loss of evolutionary history. Erwin reports that the canonical mass extinctions differed with respect to their impacts on these various metrics. For example, the end-Permian extinction had major consequences for essentially all dimensions of global biodiversity whereas the end-Ordovician extinction heavily impacted morphologic disparity but had low or medium effects on several other biodiversity measures. The biodiversity fallout from mass extinction events can vary both quantitatively and qualitatively, and the nature of each extinction influences the rate and pattern of evolutionary recovery from the catastrophe.

David Jablonski develops a somewhat similar theme in Chapter 10 by emphasizing the selectivity of mass extinctions with respect to potential risk factors such as body size, species richness, and geographic range. From a consideration of the fossil record for marine organisms (especially bivalve mollusks), the author concludes that every mass extinction event seems to show some degree of selectivity, but also that disproportionately high clade survivorship during mass extinction episodes is consistently associated with the size of the geographic range of genus-level clades. From this and other evidence, the author's take-home message is that spatial considerations are fundamental to understanding the evolutionary dynamics of biodiversity, including a clade's susceptibility to extinction and its potential for recovery and expansion following a mass extinction event. These findings have ramifications for the current biodiversity crisis because human activities are altering the geographic distributions of many taxa around the world.

In Chapter 11, John Alroy uses information from a recent web-based "Paleobiology Database" to revisit classical questions about the marine fossil record, such as: Do biotic turnovers occur in pulses that coincide with the boundaries between geological intervals? Did extinction rates decline during the Phanerozoic? Are biotic extinction rates more volatile than origination rates? Do large-scale extinctions exhibit a 26 Myr periodicity as some have claimed? Were the "Big Five" mass extinction events qualitatively distinct from lesser extinction episodes? Alroy's provisional answers to some of these questions are unorthodox. For example, he suggests that the Big Five are merely the upper end of a continuous spectrum of extinction intensities, such that it is "a matter of taste whether to speak of the Big Five, the Big Three, or just the Big One…." The analyses yield empirical estimates of typical recovery times from mass extinctions. Alroy concludes that the rebound from the ongoing mass extinction will probably take between 15 and 30 million years, if past mass extinction events are any guide.

Moving closer to the present time, late-Quaternary extinctions heavily impacted large mammals especially. The last 50,000 years were witness to the extinction of approximately two-thirds of all genera and one-half of all species of mammal weighing more than 44 kg (about the size of a sheep). Causal factors for this megafaunal extinction have been much debated, with a leading hypothesis being human hunting (overkill) arguably augmented by habitat alteration and climate change. In Chapter 12, Anthony Barnosky examines the situation from the fresh perspective of historical tradeoffs in biomass. An inverse relationship between human biomass and nonhuman megafaunal biomass indicates that before the mass extinction, the energy needed to construct large animals was divided among many species, whereas after the extinction much more of the planet's total supply of energy became concentrated in one species (*Homo sapiens*) and its domesticates. Based on the historical chronologies of biomass transitions in various parts of the world, Barnosky draws several biological implications, including how the current depletion of fossil fuels as an energy source may translate into near-future challenges for global biodiversity.

9

Extinction as the Loss of Evolutionary History

DOUGLAS H. ERWIN

Current plant and animal diversity preserves at most 1–2% of the species that have existed over the past 600 million years. But understanding the evolutionary impact of these extinctions requires a variety of metrics. The traditional measurement is loss of taxa (species or a higher category) but in the absence of phylogenetic information it is difficult to distinguish the evolutionary depth of different patterns of extinction: the same species loss can encompass very different losses of evolutionary history. Furthermore, both taxic and phylogenetic measures are poor metrics of morphologic disparity. Other measures of lost diversity include: functional diversity, architectural components, behavioral and social repertoires, and developmental strategies. The canonical five mass extinctions of the Phanerozoic reveal the loss of different, albeit sometimes overlapping, aspects of loss of evolutionary history. The end-Permian mass extinction (252 Ma) reduced all measures of diversity. The same was not true of other episodes, differences that may reflect their duration and structure. The construction of biodiversity reflects similarly uneven contributions to each of these metrics. Unraveling these contributions requires greater attention to feedbacks on biodiversity and the temporal variability in their contribution to evolutionary history. Taxic diversity increases after mass extinctions, but the response by other aspects of evolutionary history is less well studied. Earlier views

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of postextinction biotic recovery as the refilling of empty ecospace fail to capture the dynamics of this diversity increase.

Extinction is the inevitable fate of organisms, although there is considerable variance in both rates of extinction through time and the duration of particular species or clades. By some estimates, extant multicellular biodiversity is but 1–2% of all multicellular species that have existed over the past 600 Ma (Valentine, 1970; Raup, 1991). Paleontologists have long recognized that the relatively regular overturn of species is occasionally punctuated by more severe biotic crises, including at least five events recognized as mass extinctions. Some have claimed that rates of current species loss exceed those of past mass extinctions. Perhaps the most valuable contribution that paleontologists can make to understanding the current biodiversity crisis is to identify the relationship between attributes of the loss of past evolutionary history and both the depth of past crises and the speed and structure of subsequent biotic recovery. Given that conservation biologists increasingly face a problem of triage, where not all species can be saved, can paleontological data provide any insights into the species, communities, or structures that should have the highest priority for support? Paleontological data are unlikely to be decisive in such decisions, but the unique perspective provided by the fossil record may provide a useful input.

Here, I discuss a range of potential metrics for the impact of extinction on the loss of evolutionary history and provide a preliminary application of them to the five canonical mass extinctions (see also Alroy, Chapter 11, this volume). There are, however, relatively few applications of these metrics to understanding the processes of postextinction biotic recovery.

METRICS FOR THE LOSS OF EVOLUTIONARY HISTORY

The traditional accounting method for the loss of evolutionary history is taxa: populations and species for biologists, often genera or families for paleontologists because the vagaries of preservation and correlation make species-level compilations impractical. Conservation biologists have long focused on species, an approach enshrined in the U.S. Endangered Species Act. This reliance on taxa tends to assume, implicitly, that taxonomic entities are a reliable metric to the impact of extinction on ecosystem structure and function, morphological variability, behavior complexity, and developmental processes. This assumption is often far from true. Consequently, conservation biologists have proposed other metrics for identifying critical targets for conservation (Purvis and Hector, 2000), including biogeographic centers of endemic taxa, or hotspots (Meyers *et al.*, 2000), and the characterization of phylogenetic diversity (Faith, 1992a; Faith and Baker, 2006) and evolutionary distinctiveness (Vane-Wright *et al.*, 1991). There is, however, a more important reason for considering the loss of other aspects of evolutionary history, and that is the search for mechanisms underlying patterns of extinction and construction of biodiversity. Ecologists increasingly recognize the importance of a network of interactions in generating biodiversity, including positive feedback relationships among biodiversity, productivity, and stability (Worm and Duffey, 2003; Montoya *et al.*, 2006).

Although paleontologists are aware of the diversity of effects on evolutionary history caused by past extinctions, particularly mass extinctions, we have been slow to develop and apply comparative metrics beyond taxic compilations and estimates of geographic range. Enough work has been done to suggest a range of alternative metrics. Biogeographic structure is an important aspect of evolutionary history that has been considered elsewhere (Jablonski, 2007).

Taxic Diversity

The divisions of the geologic timescale are framed by biotic crises recognized by early geologists as "revolutions" triggering wholesale changes in the biota. Paleontologists have since compiled records of fluctuations in taxonomic diversity for marine taxa (Sepkoski, 1984, 1997), terrestrial plants (McElwain and Punyasena, 2007), vertebrates (Benton, 1989), and various microfossil groups (Rigby and Milsom, 2000). Patterns of extinction and origination have received considerable attention, particularly the decline in "background" extinction rates through the Phanerozoic for marine families and genera (Flessa and Jablonski, 1985) and episodic events of increased extinction. Curiously, as the English geologist John Phillips understood as long ago as the 1840s, extinctions within geologic stages appear pulsed, rather than spread out through the stage (Foote, 2005). Within clades paleontologists have also identified intriguing patterns of replacement where successive subclades replaced earlier clades. For higher-resolution analyses statistical techniques have been developed to account for sampling problems [see Jin *et al.* (2000) for an application to the end-Permian mass extinction].

Several general lessons emerge from these compilations. First, the persistent decline in extinction rates suggests an increased stability in younger taxa, although this may be a statistical artifact of increased species/genus and species/family ratios (Flessa and Jablonski, 1985). It would be of considerable interest to know whether this apparent increased robustness is real and whether it translates into some of the other metrics described below. Second, patterns of subclade replacement can suggest adaptive improvement within the activities of the larger clade, a pattern confirmed by the power of incumbency (Rosenzweig and McCord, 1991). Third, as demonstrated by a recent analysis of Cenozoic mollusks from New Zealand, species and genera exhibit a limited interval of peak abundance, followed by a long decline to extinction. In this system at least, the species at greatest risk of extinction are those already in decline (Foote *et al.*, 2007), although this does not appear to hold true during mass extinctions that may truncate ranges (Foote, 2007). Fourth, mass extinction events periodically upset these patterns, and particularly at the end-Permian mass extinction, trigger pervasive changes in patterns of ecological and evolutionary dominance. Thus over evolutionary time, episodic extinctions has been an important driver for evolution.

Understanding the processes controlling long-term changes in diversity requires identifying and correcting for biases in the fossil record that can be introduced by preservation and sampling. Consequently paleontologists have developed new approaches designed to identify and correct for such biases (Smith, 2001; Crampton *et al.*, 2003; Foote, 2003, 2007; Peters, 2005). These techniques have been applied to correct for biases in our record of the end-Ordovician mass extinction (Krug and Patzkowsky, 2004). As discussed by Alroy (Chapter 11, this volume), the diversity patterns produced by this intensive compilation of taxic diversity largely follow those of Sepkoski's earlier work (Sepkoski, 1982, 1992, 1993). This effort identifies at least three of the five canonical mass extinctions below. However, like other work (Bambach *et al.*, 2002, 2004) it raises questions about the magnitude of other extinction events.

Finally, counting taxa, whether species, genera, or families, assumes that each taxon is equivalent, which is far from true when one considers the differences in diversity or abundance within different groups, much less their evolutionary distinctiveness, morphologic disparity, ecological function, or evolutionary potential.

Phylogenetic Diversity

The two remaining species of tuatara are the sister clade to the ≈6,200 snakes and lizards of the Order Squamata, as the few remaining onycophorans are to the Phylum Arthropoda. Both onycophorans and tuataras are far more evolutionarily distinct than any two members of their sister clade, a fact not captured by a simple taxic approach. A simple exercise illustrates that identical levels of species loss can conceal very different effects on evolutionary history (Fig. 9.1). In each case roughly the same total number of species has been lost. In alternative A, however, there is little loss of the overall structure of the tree, whereas in alternative B, an entire clade has been pruned. Alternative C removes the most basal

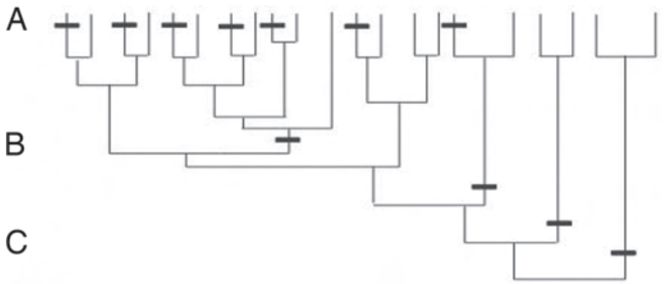

FIGURE 9.1 Similar losses of taxic diversity have very different implications for the loss of evolutionary history depending on the phylogenetic distribution of the extinctions. Three different scenarios are shown, at levels A, B, and C. (*A*) Seven taxa are lost (33% extinction) but the overall structure of the phylogeny is preserved. (*B*) An entire clade of seven taxa is pruned, but the remaining structure is preserved. (*C*) Six taxa are lost but this eliminates the deepest branching clades.

clades, each of which represents unique units with long evolutionary history. This simple example demonstrates how knowledge of the phylogenetic structure is essential to evaluating the amount of evolutionary history lost or at risk, and not surprisingly, conservation biologists have proposed several different metrics for measuring phylogenetic diversity (Vane-Wright *et al.*, 1991; Faith, 1992a; Faith and Baker, 2006). Although some have argued that taxic diversity is a reliable proxy for phylogenetic diversity, empirical studies have convincingly demonstrated the need for phylogenetic analyses. A study of the plants of the fynbos of South Africa, for example, showed that generic richness is strongly decoupled from phylogenetic diversity (Forest *et al.*, 2007). The most direct demonstration of the importance of a phylogenetic framework was a study showing that some 80% of the structure of the underlying phylogeny can survive even a 95% loss of species (Nee and May, 1997), if the extinctions are random. When the phylogenetic structure of an extinction is highly clustered, the effects on evolutionary history can be more severe (Purvis *et al.*, 2000a).

Paleontologists have long recognized the unequal impact of past biotic crises on the disappearance of particular clades, including archaeocyathid sponges in the Early Cambrian; many trilobite clades and numerous problematica during the various Cambrian crises; trilobites, blastoids, and many smaller clades during the end-Permian mass extinction; conodonts at the end-Triassic event; and nonavian dinosaurs, ammonoids, and rudist bivalves during the end-Cretaceous mass extinction. Each such disappearance removed clades of considerable evolutionary distinctiveness. The application of phylogenetic analyses remains sufficiently new that although some studies have addressed phylogenetic patterns across mass extinction boundaries, many of these are at high taxonomic level and broad temporal scope. Several studies have addressed the issue of whether phylogenetic analyses to "correct" ranges using ghost lineages provide a better estimate of diversity than a purely taxic approach [compare Norell (1993) with Wagner (2000) and Lane *et al.* (2005)], but this is a different issue from using phylogenetic analysis to understand the structure of an extinction. No studies have explicitly addressed the impact of mass extinctions on phylogenetic diversity to my knowledge. Could one develop a metric of the severity of past extinction crises based on the extent of phylogenetic diversity lost? Identifying a reliable standard of comparison will be challenging, but is likely to provide a very different perspective from taxic studies.

Morphologic Disparity

Every paleontologist is familiar with lost, unique morphologies: the "weird wonders" of the Middle Cambrian Burgess Shale fauna, or *Arthropleura*, the immense, 20-cm-wide, several-meter-long millipede of the Carboniferous. Paleontologists have characterized such morphological distinctiveness as disparity [reviewed in Foote (1997) and Erwin (2007a)]. Although paleontologists have long used ranks of the Linnean hierarchy as a proxy for disparity, quantitative analyses of form have demonstrated that neither taxonomic rank nor taxic diversity is a reliable proxy for disparity (Foote, 1993). A host of quantitative methods has been proposed to analyze different aspects of morphology, and the occupation of morphospace by particular clades, with the appropriate techniques dependent on the question being addressed, and whether continuously variable characters or meristic characters are being used (Wagner, 1995). In almost every case examined, morphometric studies of disparity have demonstrated overwhelmingly that morphospace is rapidly constructed early in the evolutionary history of major clades, with taxonomic diversification often lagging behind (Erwin, 2007a).

Patterns of disparity have been analyzed across a number of mass extinctions, principally to understand the patterns and processes involved in the reestablishment of ecospace after these crises. Despite significant reductions in disparity in the immediate aftermath of a mass extinction, studies of brachiopods, crinoids, blastozoans, and ammonoids generally demonstrate rapid reexpansion of morphospace, although often in a different region than was occupied before the extinction [Foote (1999), Ciampaglio (2002, 2004), McGowan (2004), Villier and Korn (2004), and discussion in Erwin (2007a)]. Even in clades that experience almost catastrophic decreases in diversity and disparity, such as echinoids and ammonoids during the end-Permian mass extinction, disparity can rebound to even greater levels [e.g., McGowan (2004) for ammonoids]. Critically, these studies suggest that at least within broad body plans, the developmental process does not become so increasingly constrained with time as to limit the exploration of morphospace.

Functional Diversity or Ecospace

Holling (1973) defined resilience as the magnitude of disturbance that a system can absorb before shifting to an alternative state. Ecological studies have demonstrated that the loss of biodiversity can imperil ecosystem services and functions (Loreau *et al.*, 2001, 2002; Folke *et al.*, 2004; Balvanera *et al.*, 2006; Cardinale *et al.*, 2006; Worm *et al.*, 2006), potentially leading to a negative feedback loop further reducing diversity. An assessment of experiments on grassland biodiversity (Hector and Bagchi, 2007) demonstrated a positive relationship between the number of species considered and the overall functioning of multifunctional ecosystems. These results contradict claims of ecological redundancy in ecosystem function (McCann, 2000) and suggest that many, if not most, species do play important roles in ecosystems.

The challenge in analyzing functional diversity is to establish appropriate metrics. For ecological studies Petchey and Gaston (2006) conclude that tabulating the number of functional groups or types is not reliable. Paleontologists thus face significant, although not unsurmountable, problems in identifying the ecological services and functions because the most straightforward paleontological approach is to categorize taxa of interest into different functional groups, such as carnivores, herbivores, suspension feeders, etc. Such categories can often readily be identified in fossils and can be consistent across larger taxonomic groups. Paleontologists have long discussed the selective impact of mass extinctions on trophic groups, such as the pervasive extinction of epifaunal, suspension-feeding marine taxa during the end-Permian mass extinction (Erwin, 1993).

Macroecological guilds were developed as an extension to ecological guilds, encompassing a suite of species (not necessarily related) competing for a similar resource (Bambach, 1983). The concept has primarily been applied to large-scale paleoecological trends, rather than more intensive studies of extinction episodes. One limitation of the guild approach, however, lies in identifying the critical limiting resources that define the members of a guild. A more operational concept is ecospace, which focuses on general modes of life and can be defined independently of species. For marine animals these modes of life are defined in terms of motility, or ability to respond to disturbance; tiering or relationship to the substrate (burrowers versus swimmers), and feeding strategy, or means of acquiring energy (Bush *et al.*, 2007). The six possibilities along each of these axes define a 3D grid of 216 possibilities, of which only 92 appear to be occupied (Bambach *et al.*, 2007). As with marine guilds, many different taxa can occupy each of these different modes of life, so identifying which modes are occupied across a mass extinction may not be particularly informative. One could imagine a more intensive study in which this framework was used to chronicle across mass extinction both how many modes of life were exhibited by various clades and the changing density of occupation by various clades of particular modes of life. Such a study would be particularly informative if it revealed differences in extinction intensity between different functional groups.

In some cases it may be possible to apply more rigorous analyses to the problem, such as the comparison of food web structures. Ecologists have developed a rich toolkit for studying the network properties of food webs (Martinez and Dunne, 2000), and with a working group at the Santa Fe Institute we have recently shown that such methods can be applied to Cambrian fossil communities. Although ecologists have access to direct feeding observations and gut contents in practice they often rely on morphology and other data also available to the paleoecologist. Our results demonstrate that ancient food webs can be reliably reconstructed, opening up the potential to study changes in the network properties of ecosystems across mass extinctions (Dunne *et al.*, 2008).

Modeling changes in functional diversity, trophic complexity, and food web structure in the search for patterns that can be observed in the fossil record is another approach. We developed a simple model in which extinction was simulated by the collapse of primary productivity, triggering reductions in the diversity of higher trophic levels (Solé *et al.*, 2002). The results imply that the trophic structure of extinction may influence the tempo and pattern of recovery. More detailed computer simulations of the effects of both productivity loss and resulting secondary extinctions through a food web further emphasize the importance of the network structure in the pattern of extinction (Roopnarine, 2006; Roopnarine *et al.*, 2007). Although the significance of these results is limited because of the lack of empirical input into the food web structure, it suggests something of the insights that may eventually result.

An additional area that could prove important in understanding the loss of functional diversity is the correlation between scaling relationships and ecological networks, particularly as biodiversity collapses. For example, metabolic scaling theory posits linkages across metabolic activity, form, population size, species diversity, and other variables (West *et al.*, 1997; Enquist *et al.*, 2003, 2007). The apparent relationship between metabolic activity and some mass extinctions (Bambach *et al.*, 2002; Knoll *et al.*, 2007), suggests that the relationship between scaling theory and extinction is worth exploring, as are species-energy relationships (Evans *et al.*, 2005; Hawkins *et al.*, 2007a).

Ecological networks also provide a host of services to the community, ranging from clean water to fine-scale modification of climate (microhabitats). These ecological services have been a subject of considerable interest among conservation biologists, but have not been addressed in deep time. For example, what was the impact on the water quality in shallow marine ecosystems as a consequence of the loss of so many articulate brachiopods, crinoids, bryozoans, and other filter feeders during the end-Permian mass extinction? This issue is probably best investigated through stable isotope studies of nutrient flow or geochemical cycling (West *et al.*, 2006) or where the services leave a tangible fossil record.

Architectural Diversity and Ecosystem Engineering

The framework of modern reefs is generated by scleractinian corals, with a significant contribution from coralline algae and early diagenetic cements. Architecturally similar structures, at least at a gross scale, have been built by microbial communities, sponges and archaeocyathids, tabulate and rugose corals, stomatoporoids, bryozoans, brachiopods, and rudist bivalves. Reefs are a specific example of the provisioning of architectural diversity, which can provide a positive feedback on biodiversity. Such ecosystem engineering allows species to modify the environment in ways that can affect, either positively or negatively, resource availability for other species (Jones *et al.*, 1997). A related concept is niche construction, in which species modify their own environment in a way that influences the fitness of the population and, through ecological inheritance, the fitness of subsequent generations (Odling-Smee *et al.*, 2003). Although ecosystem engineering can be recognized in the fossil record, identifying niche construction requires an understanding of selection pressures that is generally more difficult for paleontologists. Both niche construction and ecosystem engineering are currently the subject of considerable investigation and appear to have significant implications for macroevolution (Erwin, 2008).

Reef ecosystems provide a clear example where the loss of the 3D complexity of the reef has a strong negative impact on biodiversity. Kiessling (2005) showed that over million-year periods high biodiversity on reefs is related to stability, as measured by the density of skeletal organisms, the style of reef building, and the types of biotic reefs. Some mass extinction events destroy this buffering from environmental fluctuations. The composition and consequent fabric of reefs has undergone considerable variation during the 543 Ma of the Phanerozoic (Wood, 1999; Kiessling, 2002). The structure of Early Cambrian to Early Ordovician reefs was dominantly microbial. From the Middle Ordovician radiation through the Late Devonian mass extinctions, stromatoporoids (coralline sponges) and corals were the primary reef builders, with important contributions from other sponges in the early part of the interval. Latest Devonian through Early Permian reefs are often described as "mud mounds" because of the absence of abundant framework builders in these primarily algal and microbial systems. In the Early to Middle Permian, between five and seven different reef types have been described with sponges, brachiopods, corals, and bryozoans being prominent components of different types. Scleractinan corals become the major reef builders in the Late Triassic, with significant contributions from bivalves during some intervals. Indeed, post-Aptian Cretaceous reefs were built largely by rudist bivalves. Cenozoic reefs were constructed by scleractinian corals and coralline red algae. These gross patterns obscure Phanerozoic trends of changing ecology, including higher nutrient requirements toward the recent (Kiessling, 2002). An important issue for further exploration is the extent to which these different reef types were ecosystem builders that enhanced the diversity of other groups. For example, the phylloid algal mounds of the Lower Permian of West Texas apparently were so dense that they excluded many other organisms (Toomey, 1976), whereas later scleractinian reefs appear to have enhanced diversity. On land, trees and forests often provide a similar architectural structure to reefs in the ocean.

Behavioral and Social Complexity

The social and behavioral complexity of extinct animals might seem irretrievably lost (other than what might be inferred from morphology or the known history of social clades). In fact, the preservation of tracks, trails, and burrows provides insights into behavior, with the constraint that such trace fossils can rarely be uniquely associated with particular species (Seilacher, 2007). More commonly, particular trace fossils could be produced by many distantly related species. Worms of several different phyla can produce similar burrows. Nonetheless, trace fossils can provide considerable insight into the complex behavioral repertoires of their makers. Vertebrate trace fossils on land provide similar insights, for example, into herding behavior among some dinosaurs, or burrowing among Late Permian dicynodonts in South Africa (personal observation). Other evidence of behavioral complexity comes from the characteristic patterns preserved in fossil leaves by herbivorous insects, reflecting both the behavior and mouthpart morphology of various herbivorous insect groups (Labandeira, 2006). One means to track changes in behavioral complexity during a mass extinction is by documenting changes in trace fossil abundance and diversity.

Developmental Diversity

The great morphologic disparity of Cambrian and Ordovician trilobites might appear to be a paradigmatic example where we can infer the loss of great developmental diversity. Comparative studies of the genes involved in development have now demonstrated that many developmental processes are highly conserved across all bilaterian animals and some originated even deeper in time, as shown by genes with the same developmental role in cnidarians and vertebrates [summarized in Erwin (2006b); see also Raff (2007)]. This pattern of extreme conservation of developmental patterning suggests that the loss of developmental diversity caused by extinction may be less extensive than it might otherwise appear. Studies of other arthropods, coupled with detailed studies of the patterns of morphologic evolution of trilobites (including developmental information retrieved from fossilized representatives of larval stages), have demonstrated that information on developmental patterning can be recovered (Hughes, 2007). Although patterns of gene expression, much less the network of gene regulatory interactions, cannot be identified, Hughes (2007) has compared the repatterning of the cephalic and trunk regions during the Cambrian and Ordovician diversifications of trilobites. His analysis shows that the Cambrian radiation of the group involved fundamental changes in various parts of the body plan: the number of body segments, how they were formed, and in the articulations between them. In contrast, the Ordovician radiation involved morphological "embellishments" of trilobite subclades whose architectures had already stabilized.

The deep conservation of developmental processes across many clades is consistent with recent comparative studies of the evolution of gene regulatory networks, suggesting that the evolution of regional patterning systems during the initial diversification of animal body plans generated a hierarchical structure (Davidson, 2006; Davidson and Erwin, 2006). Studies from echinoderm endomesoderm formation and arthropod and vertebrate heart development have revealed a network of highly conserved regulatory genes at the core of these systems whose interaction is required for development of the relevant body parts. Surrounding this kernel of conserved regulatory interactions, however, is a network of other interactions, and downstream a set of structural genes whose activity is controlled by the network. Elements of this surrounding network are less refractory (to varying degrees) to evolutionary modification, and of course the structural genes are the locus of adaptive evolution.

If this result is generally true of metazoan developmental evolution, one implication is that although the loss of biodiversity will result in the loss of downstream elements of the regulatory hierarchy, these elements are also the most labile to evolutionary change. In contrast, kernels appear to be broadly conserved within major body plans, and in some cases across disparate groups. Consequently, loss of these kernels was likely only to have occurred during the infrequent loss of clades the equivalent of the Linnean rank of phylum or class. For marine animals this loss would have been largely during the Cambrian and again during the end-Permian mass extinctions. The loss of major clades of insects during the end-Permian might have caused a loss of some developmental diversity, but it is less clear whether unique developmental processes at the level of kernels were present. Among vertebrates there are many extinct groups of fish and early tetrapods, such as the armored fish of the Devonian and the mammal-like reptiles of the Permo-Triassic, that could have harbored now vanished developmental strategies. But as with insects, it is far from clear they were unique at the level of kernels.

Our understanding of plant developmental biology, although expanding rapidly, is less advanced than for animals, and we do not know whether a similar highly structured regulatory hierarchy exists within plants. Morphologic evidence has revealed the diversity of tree-like forms that evolved repeatedly, with many now-extinct clades using very different developmental and structural strategies to achieve a similar end. All trees need to solve the same basic problem of providing structural support while distributing nutrients vertically. Both modern pines and other flowering trees such as dogwood or oaks are constructed with an inner, woody, secondary xylem produced by the vascular cambium and surrounded by phellem. But cycads are constructed of an inner pith and an outer cortex, with much of the structural support on the outside from persistent leaf bases. Arborescent lycopsids, horsetails in the Carboniferous, tree palms, and tree ferns each have distinct ways of forming trees. Yet each of these different types of trees was adapted to a particular suite of environmental conditions, which influenced the nature of the resulting communities (Niklas, 1997; Donoghue, 2005). Thus it seems likely that major developmental strategies of plants have disappeared, particularly during the late Paleozoic.

APPLICATION TO PAST BIOTIC CRISES

Applying some of these different aspects of diversity to past mass extinctions is difficult because of both lack of data and difficulties in establishing appropriate criteria and reproducible metrics, but identifying these different measures of diversity is the first step toward building a more robust and quantifiable approach. Table 9.1 provides a preliminary, somewhat impressionistic, application of these metrics for marine animals across the five classic mass extinction intervals. In the absence of more comprehensive tools, proxies are used for some categories such as reefs for architectural diversity and trace fossils for behavioral complexity.

TABLE 9.1 The Effect on Different Measures of Diversity for Marine Organisms During the Five Canonical Mass Extinction Episodes of the Phanerozoic

Diversity	Ordovician	Devonian	Permian	Triassic	Cretaceous
Taxic	60/26%	57/22%	82/52%	53/22%	47/16%
Phylogenetic	?	?	High	?	? Medium
Morphologic	High	Medium	High	?	? Medium
Functional	Medium	High	High	Low	Medium
Architectural	Medium	High	High	Medium	Low
Behavioral	?	?	High	Medium	Medium
Developmental	Low	?	Medium	?	?

NOTES: Taxic diversity drops are shown for genera and families from Sepkoski (1996). Estimates of loss of phylogenetic diversity are based on the loss of major clades, as documented by phylogenetic analyses; morphologic disparity is assessed within particular clades, and the loss of major clades; functional diversity is assessed based on published paleoecological studies. Loss of architectural diversity is measured by changes in reef volume and the diversity of reef ecosystems (Wood, 1999; Flügel and Kiessling, 2002). Changes in behavioral diversity were assessed by changes in the complexity of trace fossil assemblages. Developmental diversity was assessed as described. Question marks indicate an absence of sufficient data.

Estimates of the loss of family and generic diversity are from Sepkoski (1996).

One perplexing aspect of the end-Ordovician mass extinction (490 Ma) is that although it is the second largest loss of taxic diversity of marine organisms it had relatively little ecological impact in most groups (Droser *et al.*, 2000). Limited phylogenetic analyses have been produced, mostly for graptolites and gastropods, although some broader studies do span the boundary. The loss of morphologic disparity during this event appears to have been high, whether as measured by the major losses among graptolites, conodonts, brachiopods, and possibly nautiloids or by more quantitative studies of disparity within major clades (Foote, 1991, 1994a; Ciampaglio, 2002, 2004). Using reefs as our measure of architectural complexity, there is a major loss of both reef types and carbonate production although there is little ecological impact (Wood, 1999; Flügel and Kiessling, 2002), hence the medium ranking in Table 9.1. Twitchett and Barras (2004) record only a single study of trace fossils through this interval, too little to estimate the impact on behavioral complexity. Finally, as no major clades completely disappeared the loss of developmental diversity at this time appears to have been fairly low. What developmental complexity was lost was likely in the terminal portions of the networks rather than the highly conserved cores.

The Late Devonian mass extinctions were a series of events best expressed in rocks of Europe (McGhee, 1996). The loss of morphologic disparity seems to have been intermediate, both in terms of the loss of major clades and for the few clades where disparity has been quantitatively assessed. Reef builders were heavily impacted by this episode, with colonial tabulate corals virtually disappearing as significant constructors. Together with the significant loss of stromatoporoids, this extinction caused a major shift in reef types that persisted into the Permian (Wood, 1999; Flügel and Kiessling, 2002). There are too few studies of this event on which to assess its impact on phylogenetic, behavioral, or developmental diversity.

Two major extinction episodes close out the Permian, one at the end of the Guadalupian, of which much less is known, and the most severe mass extinction of the Phanerozoic at the close of the Permian (Erwin, 2006a). The loss of taxonomic diversity during this interval was higher than during any other event, some 82% of marine genera and 54% of marine families (Sepkoski, 1996). Phylogenetic analyses of articulate brachiopods, bryozoans, and gastropods reveal a considerable loss of diversity. The impact on morphological disparity is apparent from the large number of clades lost (trilobites, blastoids, and the tabulate and rugose corals) or severely affected (articulate brachiopods, echinoids, ammonoids, radiolarians, bryozoans, and foraminifera). The loss of disparity is confirmed by quantitative studies of disparity among brachiopods (Ciampaglio, 2004), ammonoids (McGowan, 2004), and crinoids and blastoids (Foote, 1992, 1999). Carbon isotopes indicate a significant loss of primary productivity (Jin *et al.*, 2000) that persisted for ≈2 million years (Payne *et al.*, 2004; Erwin, 2007b). The most pervasive indication of the functional and ecological impact of this extinction was that the marine communities of the Ordovician-Permian, dominated by epifaunal, suspension feeding brachiopods, byozoans, and pelmatazoan echinoderms, simply vanished (Erwin, 2006a). A large suite of reef types had developed by the Middle Permian, virtually all of which disappeared, leaving a gap in metazoan-constructed reefs during the Early Triassic (Wood, 1999; Flügel and Kiessling, 2002). Detailed investigations of trace fossils have revealed a significant loss of diversity with only a few types of shallow burrows occurring in earliest Triassic sections (Twitchett and Wignall, 1996; Twitchett and Barras, 2004). I have ranked the loss of developmental diversity as moderate because of both the loss of major clades and major subclades.

In the Late Triassic, ammonites and bivalves experienced the greatest extinction. There are few studies on which to assess the extent of loss of phylogenetic or developmental diversity or morphologic disparity. Although there are few studies of paleoecological patterns across this boundary, much less studies of food web structure, there is little evidence for major disruptions of functional diversity except among reefs, where a major drop in sea level triggered a substantial decline in reef volume and a somewhat less substantial drop in diversity (Flügel and Kiessling, 2002). Trace fossils have been studied in different regions, but the impact of the extinction varies between localities, in part because of shifts in the environments of deposition at the same time as the biotic crises. There is, however, evidence of some decrease in the complexity of trace fossil assemblages that cannot be attributed simply to changes in the sedimentary environment in which they were deposited.

The end-Cretaceous mass extinction led to the disappearance of significant numbers of foraminifera and other plankton and a significant drop in primary productivity (D'Hondt *et al.*, 1998). Ammonoids finally disappeared, as did belemnites and rudist bivalves. The loss of rudists was the major loss among reef biota, and Flügel and Kiessling (2002) record few other impacts among reef ecosystems. Studies of the complexity of trace fossils across this interval are relatively few and suggest only moderate impact by the mass extinction (Twitchett and Barras, 2004).

Although not one of the canonical five mass extinction episodes, extinction rates measured by taxic diversity were high during a number of stages of the Cambrian, sorting out the winners and losers among the Cambrian diversification of animals. Indeed by some metrics, particularly morphologic disparity and developmental diversity, these events may have winnowed a greater degree of evolutionary history than any of the subsequent biodiversity crises of the Phanerozoic.

THE (RE)-CONSTRUCTION OF DIVERSITY

Empty ecological space has long been considered a key factor in evolutionary innovations, as an unexploited opportunity opened by new adaptations, a new geographic region with underexploited resources, or an environment opened up through environmental change. Recoveries from mass extinctions have been viewed as encompassing each of these possibilities, as the removal of previously dominant clades provides opportunities for expansion, including by migration, of minor groups and the origin of new clades, as an increased likelihood for success of adaptations that might have been blocked, and as an instigator of environmental change that might favor new groups. What the economist Joseph Schumpeter described as "creative destruction" is true of evolution: continuing biotic overturn and more comprehensive biodiversity crises have been a normal part of the history of life, and perhaps essential to the success of evolutionary innovations.

Two principal classes of models have been applied to understanding the underlying processes of taxic diversity (Benton and Emerson, 2007). The first class includes global-level correlates of population growth models that invoke logistic growth models and either global carrying capacities (Raup, 1972; Carr and Kitchell, 1980) or coupled logistic models. One example is Sepkoski's description of the diversity patterns of the Cambrian, Paleozoic, and Modern evolutionary marine faunas (Sepkoski, 1984); see Alroy (2004) for a critique. The alternative class was labeled expansionist by Benton and Emerson (2007) as it does not invoke an explicit carrying capacity, or it suggests that it may never have been reached, possibly because of recurrent disturbances (Valentine and Walker, 1986; Benton, 1997; Stanley, 2007). The utility of a global carrying capacity is extremely doubtful (Benton and Emerson, 2007; Stanley, 2007; del Monte-Luna *et al.*, 2004).

The critical question for understanding biotic recoveries is in understanding how the network of ecological and environmental interactions facilitates the construction of biodiversity, which is a network issue, not one that is properly addressed by borrowing models of population demography. Thus understanding the growth of taxic diversity after mass extinctions requires understanding the ecological relationships that build these networks, including both the positive feedbacks (such as niche construction and environmental engineering) and the more commonly invoked negative feedbacks such as competition. At present we have no theoretical models applicable to this problem.

Our knowledge of the response of most of the other metrics during postextinction biotic recoveries is generally even more fragmentary than our knowledge of their behavior during the extinctions. The highly uneven branching structure of most phylogenetic trees reflects uneven rates of diversification along different branches of a tree and the loss of some branches through extinction (Nee and May, 1997). With the exception of the substantial literature on the relationship of the bird and placental mammals across the Cretaceous-Tertiary boundary, there are relatively few large-scale phylogenetic studies of post-mass extinction biotic recoveries. Despite this absence, many evolutionary radiations of single clades are well studied during biotic recoveries. Examples include trilobites in the Late Cambrian, ammonoids after the Late Devonian, end-Permian, and end-Triassic episodes, and quillworts in the Early Triassic. As discussed above, where it has been studied among marine taxa, morphologic disparity rapidly expands after mass extinctions (Erwin, 2007a). Significantly for the structure of these recoveries, disparity often expands into different dimensions than were occupied by the preextinction taxa, demonstrating that recoveries have their own dynamic and are not simply the refilling of previously occupied morphospace. Without detailed studies, my impression is that architectural diversity as measured by the reappearance of framework-bound reefs is often one of the last segments of diversity to rebound, and in almost all cases (the Early Jurassic is a possible exception) does so by the appearance of new groups. This apparent delay could reflect the fact that a considerable ecological network needs to be constructed, in appropriate environmental settings, before such architectural diversity can succeed.

Although there are a growing number of case studies of biotic recoveries after mass extinctions and some smaller biotic crises, our theoretical understanding of increases in taxic diversity remains lacking, as does our knowledge of the response of some of the other diversity metrics described here and the factors underlying them. One hesitates to suggest that there is a considerable empty niche here for future research.

CONCLUSION

This survey of mass extinction episodes illustrates that different metrics capture different dimensions of the loss of evolutionary history. Although these extinction events have been defined by loss of taxic diversity, this metric often captures only one perspective on the loss of biodiversity and evolutionary history. Indeed, debates continue among paleontologists about whether some of these episodes (particularly the Late Devonian and end-Triassic) actually constitute mass extinctions on the scale of the end-Permian and end-Cretaceous events. Fully appreciating the extent of the loss of evolutionary history during any biodiversity crisis requires a more complete accounting of other dimensions of biodiversity, a task that is in its infancy for some of the metrics discussed here.

The metrics of past loss of evolutionary history may provide some insights into more recent events. Although this survey illustrates that the available data on these various metrics are often meager, enough information is available to suggest that the loss of different aspects of evolutionary history may portend very different outcomes for recovery. For example, if architectural diversity is lost early in a biodiversity crisis one might expect greater loss of other aspects of diversity than if architectural diversity remains high. Empirical investigations of such effects will require very high-resolution studies, but may be possible in the Cenozoic. This is clearly an area where well-designed modeling studies may prove useful.

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10

Extinction and the Spatial Dynamics of Biodiversity

DAVID JABLONSKI

The fossil record amply shows that the spatial fabric of extinction has profoundly shaped the biosphere; this spatial dimension provides a powerful context for integration of paleontological and neontological approaches. Mass extinctions evidently alter extinction selectivity, with many factors losing effectiveness except for a positive relation between survivorship and geographic range at the clade level (confirmed in reanalyses of end-Cretaceous extinction data). This relation probably also holds during "normal" times, but changes both slope and intercept with increasing extinction. The strong geographical component to clade dynamics can obscure causation in the extinction of a feature or a clade, owing to hitchhiking effects on geographic range, so that multifactorial analyses are needed. Some extinctions are spatially complex, and regional extinctions might either reset a diversity ceiling or create a diversification debt open to further diversification or invasion. Evolutionary recoveries also exhibit spatial dynamics, including regional differences in invasibilty, and expansion of clades from the tropics fuels at least some recoveries, as well as biodiversity dynamics during normal times. Incumbency effects apparently correlate more closely with extinction intensities than with standing diversities, so that regions with higher local and global extinctions are more subject to invasion; the latest Cenozoic temperate zones evidently received more invaders than the tropics or poles, but this dynamic could shift dramatically if tropi-

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cal diversity is strongly depleted. The fossil record can provide valuable insights, and their application to present-day issues will be enhanced by partitioning past and present-day extinctions by driving mechanism rather than emphasizing intensity.

The inventory of life on Earth has always been determined at the most basic level by the difference between origination and extinction. This fundamental macroevolutionary equation, richness = origination – extinction, has been formally applied in many ways and with many elaborations, but takes on special consequence when attempting to evaluate the processes shaping present-day biodiversity, where neither term in the right side of the equation can be observed directly. Some progress has been made in modeling these parameters, but most approaches involve strong assumptions, require very large datasets, and carry large uncertainties [e.g., Paradis (2004), Ricklefs (2007a,b)]. The spatially explicit form of this equation, where richness is a local or regional pool of species or higher taxa, and immigration and emigration terms enter the right side of the equation (Jablonski *et al.*, 2006), is important in many situations, from biotic responses to Pleistocene climate cycles and ongoing climate changes to recoveries from mass extinctions. However, this form is even more difficult to apply rigorously without historical data, and my emphasis here will be on the fossil record. Few would argue against the idea that the spatial fabric of extinction has shaped, and will continue to shape, the biosphere in profound ways, but spatial effects have been neglected relative to temporal patterns (partly because documentation is so challenging). I will argue that the insights beginning to emerge from spatially explicit approaches to ancient extinctions have significant implications for the dynamics of diversity of the past and in the future.

This discussion will encompass a range of extinction intensities and focus on marine systems, where the fossil record is richest: application of these generalizations to terrestrial realms requires more study. Opinions are divided on whether the handful of mass extinctions of the geologic past are a separate class of intensities from the "background" extinction that constitutes the great bulk of geologic time [and the bulk of total extinction; Raup (1994)], but this is a secondary issue that can probably be resolved by factoring out the well-known secular decline in background extinction rates (Bambach *et al.*, 2004; Jablonski, 2005; Stanley, 2007). As discussed below, extinction selectivities evidently shift between episodes of low and high extinction rates, and this selectivity is the more important issue for understanding the role of extinction in shaping past and future biotas. I will corroborate previous evidence for a strong spatial component to survivorship during major extinction events, present a multifactorial analysis of the end-Cretaceous (K-T) mass extinction in which geographic range emerges as the best predictor of survivorship in marine bivalves, and argue that such indirect effects are probably more important than generally appreciated. I will also discuss regional variations in the balance of invasions and local origination in the aftermath of the K-T event, which are somewhat unexpected given that the extinction itself tended to increase biotic homogenization on a global scale by preferentially removing the more localized taxa. Invasions and extinctions are also important during times of "normal" extinction intensities, as I will illustrate with reference to the dynamics of the latitudinal diversity gradient. I will conclude with some implications for integrating insights for past and present-day extinctions and suggest that a powerful approach might involve comparative dissection in extinction patterns according to likely drivers. Throughout I will note gaps in our understanding that would benefit from combined study of modern and ancient systems.

In this chapter, I will focus mainly on marine bivalves such as mussels, scallops, and cockles. Bivalves are becoming a model system for the analysis of large-scale biogeographic and evolutionary patterns (Crame, 2000, 2002; Jablonski *et al.*, 2003b, 2006; Kidwell, 2005; Valentine *et al.*, 2006; Krug *et al.*, 2007) for several reasons. They are taxonomically rich but not unmanageable (≈3,000 living and fossil genera), and their systematics are increasingly understood, so that taxonomic standardization and phylogenetic treatment of heterogeneous data are feasible. They have diverse life habits, from filter-feeding to photosymbiosis and chemosymbiosis to carnivory. They occur at all depths from the intertidal zone to deep-sea trenches and from the tropics to the poles. They are abundant and often well preserved as fossils [although not all habitats and clades are equally represented; Valentine *et al.* (2006)], and they have diverse shell mineralogies and microstructures, which allows analyses to control statistically for, and thus factor out, some, although not all, of the biases in the fossil record (Kidwell, 2005; Valentine *et al.*, 2006). These favorable attributes do not mean that the bivalve fossil record is perfect, and preservation and sampling biases must always be considered in large-scale analyses [see, for example, the variety of approaches in Alroy (2000), Foote (2003), Bush and Bambach (2004), Bush *et al.* (2004), Jablonski *et al.* (2006), and Smith (2007)]. However, our growing knowledge of living and fossil bivalves, including the taxonomic, preservational, and geographic factors that can distort their fossil record, makes this group an excellent vehicle for integrating present-day and paleontological diversity dynamics.

EXTINCTION SELECTIVITY CHANGES AT THE MOST EXTREME EVENTS

A broad array of organismic and clade-level traits enter into extinction risk for present-day species. For example, in evaluating extinction risk in present-day terrestrial vertebrates, Purvis and colleagues (Purvis *et al.*, 2000b, 2005a; Davies *et al.*, Chapter 14, this volume) found mixed, but significant, effects for body size, a consistent inverse relation between extinction risk and both abundance and geographic range, and either a positive relation or no effect for habitat specialization. Similar patterns are seen in the fossil record. For example, the geographic range is a significant determinant of Cretaceous and Cenozoic molluscan species duration or survivorship [Hunt *et al.* (2005) and Jablonski and Hunt (2006) and references therein], and Paleozoic crinoids show a significant positive relation between habitat breadth and species duration (Kammer *et al.*, 1998). Predictable interactions among factors can also be seen, although this aspect needs much more work. Molluscan genera containing many widespread species tend to be more extinction-resistant, with a median duration of 130 million years (Myr), than genera having just a few, localized species, which show a median duration of 32 Myr, and the genera with the other combinations give intermediate values (Jablonski, 2005). These are not theoretically surprising results, but it is encouraging that the paleontological outcomes so clearly match expectations.

Extinction selectivity appears to change significantly at the most severe mass extinctions, however. The rules of survivorship changed during the K-T extinction, such that species-richness and species-level range failed to predict genus survivorship, singly or in concert [Jablonski (1986a, 2005) and see Kiessling and Baron-Szabo (2004) for comparable results for K-T corals]. In fact, survivorship of marine invertebrates in the K-T mass extinction is unrelated to a number of factors that have been shown or hypothesized to be important during more normal times. Besides the two already mentioned, these factors include local abundance, mode of larval development (which is in turn related to fecundity and species-level dispersal capability), estimated generation time, living position relative to the sediment–water interface, and trophic strategy (Jablonski, 2005).

Despite this loss in effectiveness of a variety of organismic, species- and even clade-level traits, survivorship at mass extinction boundaries is not random. Every event seems to show some degree of selectivity, but one factor that seems to have promoted survival for most major groups and most mass extinctions is broad geographic distribution at the clade level (i.e., genera), regardless of species-level geographic ranges. This effect, which has been recorded for many groups and all of the major mass extinctions [see Jablonski (2005) for a tabulation], is again further corroborated in an extensively revised version of Jablonski and Raup's (1995) data on K-T bivalves (Fig. 10.1*A* and *B*). This is more than a simple binary effect: bivalve genus extinction is inversely related to geographic range, with strong concordance between the new and old data (Fig. 10.1C). The 70% extinction suffered by the genera found in just one or two biogeographic

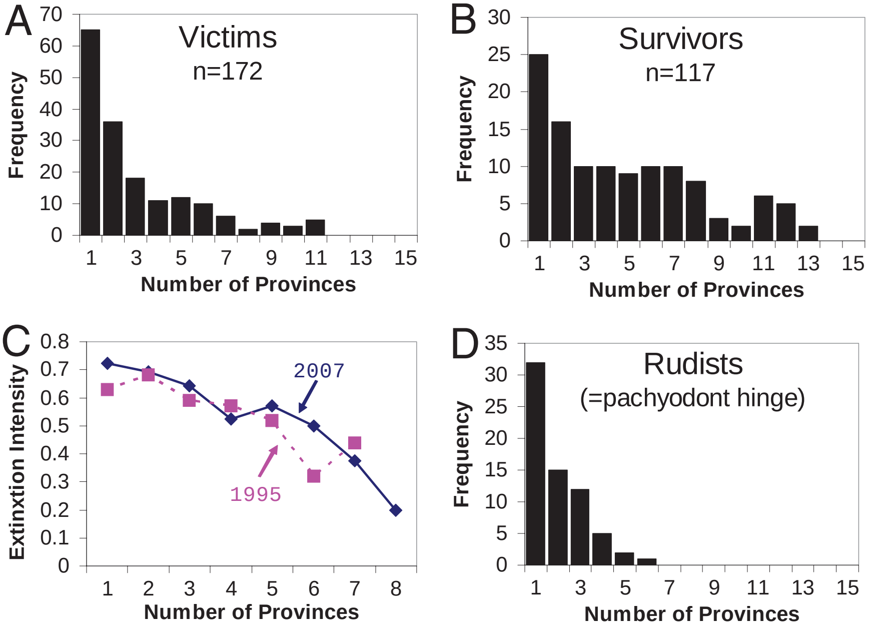

FIGURE 10.1 Spatial effects in the end-Cretaceous (K-T) mass extinction for marine bivalve genera. (*A*, *B*, and *D*) Victims of the K-T extinction (*A*) tended to be significantly less widespread than surviving bivalve genera (*B*), as measured by the number of biogeographic provinces they occurred in during the Maastrichtian stage just before the event [Mann–Whitney *U* test, $P = 0.00001$; new analysis based on an extensive, in-progress revision and update of Jablonski and Raup (1995), omitting rudist bivalves (*D*) as before, note that their inclusion as narrow-ranging victims would strengthen this result]. Adding provinces to fill gaps in observed geographic ranges strengthens the separation between victims and survivors (75% of victims are unchanged in range size and their median range is unchanged at two provinces; 60% of survivors are unchanged and their median increases from four to five provinces). Some caution is needed, because the proportion of survivors is likely to increase with phylogenetic analysis and further taxonomic standardization of early Cenozoic bivalves, but the major pattern is unlikely to change. (*C*) Significant inverse relation between extinction intensity and the number of biogeographic provinces occupied by bivalve genera during the K-T extinction (Spearman rank test, $P < 0.01$). Solid line indicates analysis of revised dataset ($n = 289$ genera). Broken line indicates analysis of previous version of dataset [Jablonski and Raup (1995); $n = 297$ genera; 28 genera were added and 36 genera were removed in the revision]. (*D*) Loss of a major adaptation (the pachyodont hinge) by hitchhiking on geographic distribution. The unique pachyodont hinge structure disappeared with the extinction of these genera at the K-T boundary, signaling the termination of the rudist bivalves (Order Hippuritoida).

provinces is significantly higher than the 20% losses seen for genera found in eight or more provinces [of a global total of 16; following Jablonski and Raup, 1995)]. That said, even 20% represents a major, and highly unusual, drawdown of diversity in this most extinction-resistant part of the biota, equivalent to losing 20% of the most widespread genera in the sea today, such as the mussels (*Mytilus*, *Modiolus*) and the scallops (*Pecten*, *Chlamys*). [Although not ideal in some respects, analyses were conducted at the provincial scale rather than based on occurrences at individual localities, because clades are distributed not along simple linear coastlines, thereby undermining the use of linear distances or simple latitude/longitude extremes. Binning by province also damps some aspects of sampling and taxonomic uncertainty at the genus level, the range-endpoints of present-day molluscan genera tend to cluster at province boundaries (Campbell and Valentine, 1977; Roy *et al.*, 1996), and the results are robust to different approaches to quantifying province-based range sizes.]

Multifactorial analyses corroborate the importance of clade-level distribution in determining survival during mass extinctions and show the value of testing for interaction among factors. For example, if variables are treated independently in the updated K-T dataset, geographic range remains the most important factor in clade survivorship, but species richness also appears to play a significant role (and body size is insignificant as a survivorship predictor). However, multiple logistic regression models taking the three variables simultaneously into account, using Akaike's Information Criterion (AIC) as a basis for model selection (Burnham and Anderson, 2002), shows species richness to covary with range such that when range is factored out, richness has an insignificant effect on survivorship ($P = 0.85$, as opposed to $P = 0.002$ for clade range, in the multiple-factor model). Body size also enters into the multiple-factor model as a weak, but significant, variable, but the multiple-factor model does not have significantly more explanatory power than the geographic range model alone, according both to the similar AIC weights (Table 10.1) and a likelihood ratio test [$P = 0.09$; see Hosmer and Lemeshow (2000)]. Multivariate approaches will help clarify patterns of extinction selectivity, even if, as here, they show that survivorship virtually collapses to the single variable of geographic range for K-T bivalves. The overlapping variation in range size among the victims and survivors suggests, however, that additional factors, or strong stochastic elements, enter into the fates of individual clades.

Widespread clades are probably always extinction-resistant compared with narrow-ranging relatives. However, during times of low extinction intensity, range is evidently just one significant feature among many, becoming increasingly important as the crowd of factors influencing taxon duration falls away as intensity mounts. How the relation between range

TABLE 10.1 Testing Models for Bivalve Genus Survivorship During the K-T Mass Extinction

Models	No. of Parameters	AIC	Weight	*P*
G** + R + B*	4	347.9	0.58	0.002/0.85/0.03
Geographic range***	2	348.6	0.40	e-6
Species richness***	2	356.2	0.02	0.0001
Body size	2	373.5	e-6	0.94

NOTES: When geographic range (G), species richness (R), and body size (B) are analyzed as independent factors, G is the most important factor, but R is also significant. When the three are analyzed together, R is not a significant factor. Note that the combined model is not significantly better than geographic range alone according to the AIC (for model selection, which essentially weighs the adding of parameters against the improved explanatory power of each model). *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

and extinction risk varies with extinction intensity is not known and is difficult to assess. The few available data suggest that the relation between extinction probability has a steep slope during times of low extinction intensity, with the most widespread genera suffering negligible extinction at those times (Payne and Finnegan, 2007; Powell, 2007a) (Fig. 10.2*A*). The simplest view would be that perturbations generally operate at too small a spatial scale to affect these most widespread elements of the global biota. In the major mass extinctions, the *y*-intercept increases, so that a greater fraction of taxa are lost from all range classes, and the slope probably decreases (Fig. 10.2*B*). This configuration is much more demanding of the data, so that sparse or noisy data may fail to capture that shallower

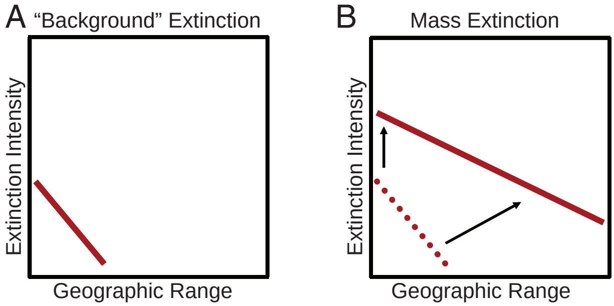

FIGURE 10.2 The inverse relation between geographic range and extinction risk appears to vary with severity of extinction. Conceptual model for this variation, such that both slope and intercept may change between times of background (*A*) and mass extinction (*B*).

slope. We know little about whether the slope and intercept change continuously or shift abruptly at thresholds. For obvious reasons, including some very practical ones relating to the present-day biota, this would be good to know.

We also know relatively little about the determinants of geographic range size at the clade level. Organismic traits such as dispersal ability and ecological strategy must play a role, but interactions with biogeographic context, clade history, and many other factors, including the way that clades extend their ranges by speciation across barriers, serve to decouple geographic ranges at the species and clade levels. For example, the geographic ranges of the 213 marine bivalve genera present today at shelf depths on the eastern Pacific margin from Point Barrow, Alaska to Cape Horn, Chile are not significantly related to the median or maximum ranges of their respective constituent species (Jablonski, 2005). Genera can attain broad ranges via a few widespread species, a mosaic of nonoverlapping but narrow-ranging species, or any combination thereof, each apparently equivalent in a mass extinction event (although this equivalence deserves further study). Genus ranges are not simply species attributes writ large, but involve a dynamic that is set at another hierarchical level, by the complexities of speciation, species extinction, and range expansion.

This strong spatial component to extinction selectivity suggests that survival can be determined by features that are not tightly linked to the organismic and species-level traits that are favored, indeed shaped, during times of lower extinction intensities. Even well-established clades or adaptations could be lost simply because they are not associated with those few features that enhance survivorship during unusual, and geologically brief, high-intensity events. As discussed below, the removal of incumbents and the subsequent diversification of formerly marginal taxa are essential elements of the evolutionary dynamic fueled by major extinctions [see also Erwin (2001), Jablonski (2001, 2005), and Erwin, Chapter 9, this volume].

These results also suggest that hitchhiking effects may be mistaken for direct selectivity more often than generally appreciated. Biological traits tend to covary, even across hierarchical levels, and so selection on one feature can drag others along with it, hampering efforts to pinpoint cause and byproduct. Such hitchhiking was detected for bivalve species richness in Table 10.1. Whenever widespread or restricted taxa tend to occupy nonrandom regions of phenotype space, for example in body sizes, trophic habits, or metabolic rates within a major group, hitchhiking becomes a real possibility, an interesting interaction across hierarchical levels where the extinction probabilities of organism-level characters are conditioned by clade-level properties (Jablonski, 2007). For example, the rudist bivalves of the Cretaceous seas (Order Hippuritoida) represent an extreme repatterning of the bivalve body plan, with highly modified conical shells and a unique, pachyodont hinge structure (Skelton, 1985; Seilacher, 1998). This clade and its bizarre growth form, including the pachyodont hinge, disappeared in the K-T mass extinction (Steuber *et al.*, 2002), but this loss was probably related less to any disadvantage inherent in the remarkable hinge apparatus than to the restricted ranges of rudist clades (Fig. 10.1*D*), and perhaps to their reliance in at least some instances on photosymbionts [Seilacher (1998), but see Steuber (2000)], as seen in modern reef-building corals. If the range-frequency distribution of rudists played a role in their demise, with correlated morphologies carried along, then we would expect a similar pattern for the other bivalve orders. This is in fact the case: the five bivalve orders with median genus ranges of one or two provinces suffered significantly more severe K-T bottlenecks (median = 93% genus extinction) than the four orders with median genus ranges of three or more provinces (median = 32% genus extinction; Spearman's rank correlation of median genus range and extinction intensity for orders = 0.74, $P = 0.02$), as predicted by the hitchhiking argument for rudists. More detailed analyses must await a morphometric or discrete-character study combined with a well-resolved phylogeny of bivalve genera, and these results suggest that such studies would be worthwhile.

The hitchhiking of such striking adaptations on the less flamboyant features that actually determine extinction resistance is probably pervasive, both during background times [hence the large literature on comparative methods and phylogenetic autocorrelation; e.g., Freckleton *et al.* (2002) and Paradis (2005)] and during mass extinctions. For example, marine bryozoan genera with complex colonies suffer more severely during mass extinctions than simple genera, but colony complexity is also inversely related to genus-level geographic range (Anstey, 1978, 1986), which may well be the ultimate basis for differential survival during the end-Ordovician mass extinction. The end-Ordovician extinction also preferentially removed snails with broad selenizones providing access to the mantle cavity, and planktonic graptolites with multiple stipes creating complex pendant colonies; the K-T extinction also preferentially removed bivalves with schizodont hinges (trigonioids), echinoids with elongate rostra (a clade of holasteroids), cephalopods with complex sutures (ammonites), and a major clade of birds with foot bones that fused from the ankles to the toes (Enantiornithes). All of these losses or severe bottlenecks are more likely to represent correlations, not necessarily with geographic range, but with some other organismic or higher-level factor, rather than direct selectivity on the most striking morphology or functional trait. These extinctions nonetheless truncated or rechanneled evolutionary trajectories through morphospace, and additional examples are plentiful.

SOME EXTINCTIONS ARE SPATIALLY COMPLEX

The K-T extinction is remarkably homogenous on a global scale, except perhaps for greater intensity in tropical carbonate settings (Raup and Jablonski, 1993; Jablonski, 2005). However, other extinction events, particularly those that are less severe on a global scale, tend to show more spatial structure. For example, the mid-Cretaceous (end-Cenomanian) marine extinction appears to have been concentrated in northern Europe and the Western Interior Seaway of North America. The smaller events in the geologic record must be interpreted critically, because at least some of them may represent, or at least be heavily overprinted by, sampling variations [e.g., Foote (2003) and Smith and McGowan (2007)]. However, a seemingly genuine extinction pulse or regional series of pulses occurs in the oceans near the start of the Pleistocene. These regional extinctions are generally taken to represent a culling of taxa unable to cope with the onset of rapid, high-amplitude climate swings and oceanographic shifts that typify the Pleistocene. They vary in intensity and occur at slightly different times among regions [e.g., Kitamura *et al.* (2000), Monegatti and Raffi (2001), Todd *et al.* (2002), Smith and Roy (2006), Rivadeneira and Marquet (2007)], perhaps owing to regional variations in the timing of oceanographic transitions toward a glacial state [e.g., Ravelo *et al.* (2004)]; the many subsequent glacial-interglacial cycles evidently drove few extinctions in marine or terrestrial settings [e.g., Huntley (2005)].

This spatial structuring of Plio-Pleistocene extinctions is interesting from many perspectives, but perhaps the most urgent need is to understand the dynamical consequences of these extinctions, which bear directly on the path of future biodiversity. Do these events reflect the setting of a new regional diversity level, such that taxa capable of weathering the volatile Pleistocene climate regime are more generalized and thus structure a biota capable of accommodating fewer species and clades? [See Valentine (1983) and Valentine *et al.* (2008) for a view of diversity-dependent factors that would favor this explanation.] Or do some regions incur a "diversification debt," a more positive analog to the extinction debt sometimes inferred for modern biotas squeezed into refugia too small to accommodate their present richness? The rapid recovery of diversity in the Caribbean, which evidently suffered more severely than the tropical eastern Pacific just on the other side of the Panama Isthmus (Todd *et al.*, 2002), suggests that at least some Plio-Pleistocene extinctions involve diversification debts rather than diversity resettings. [By this argument, the anomalously low diversity of the Southeast Pacific molluscan fauna (e.g., Rivadeneira and Marquet, 2007) is a transient effect rather than a permanent biogeographic feature, attributable perhaps to the lower rates of diversity accumulation in extratropical regions; cf. Jablonski *et al.* (2006).] However, the spatially explicit form of the fundamental macroevolutionary equation shows that regional diversity can accrue either by *in situ* origination or invasion (immigration). The high present-day rate of anthropogenic introductions in marine systems will likely outstrip regional evolutionary recovery by an order of magnitude or more, exacerbated of course by other anthropogenic stresses [e.g., Ruiz *et al.* (2000), Jackson *et al.* (2001), Lötze *et al.* (2006)]. This paleontological perspective on regional marine biodiversity adds another element to the urgency of slowing anthropogenic homogenization of marine biotas, if the diversification debt of some regions indeed makes them more susceptible to invasions (and see below).

RECOVERIES ARE ALSO SPATIALLY COMPLEX

Most research on spatial dynamics has focused on extinctions, but evidence is accumulating for a spatial component to recoveries as well. The raw evolutionary material that survives the mass extinction filter is crucial in shaping the postextinction world. However, the evolutionary novelties and the ecological restructuring that emerge in the postextinction interval, including the little-appreciated process of sorting survivors into winners and losers (Jablonski, 2002), may be as important as the extinction filter in determining the long-term trajectory of individual clades.

Returning to the spatially explicit form of the fundamental macroevolutionary equation, we can partition a regional biota after, e.g., the K-T mass extinction, into survivors of the event, locally evolved new taxa, and invaders. The four regions with the best marine molluscan records in the 10 Myr after the K-T event differ significantly in their recovery dynamics (Jablonski, 1998). For example, the North American biota was much more subject to invasions during the early stages of the post-Cretaceous recovery, and contains significantly fewer novel taxa, than the other regions. However, the survivor components (the regional extinction intensities) are indistinguishable among regions (Fig. 10.3).

Spatial heterogeneity has recently being detected for other recoveries as well. For example, after the end-Ordovician extinction ≈445 Myr ago, Baltica, a continental plate centered ≈30° south, had the lowest extinction intensity and the lowest invasion intensity among marine invertebrates, whereas Laurentia, which was straddling the equator, showed a tighter bunching of the three faunal components (Krug and Patzkowsky, 2007). Spatial heterogeneity in recovery from the huge end-Permian extinction has been reported for some groups [e.g., brachiopods and bivalves (Chen *et al.*, 2005; Bonuso and Bottjer, 2008)] but not others [e.g., ammonoids (McGowan, 2005), but see Brayard *et al.* (2006)].

The K-T example is striking in its failure to show the inverse relation between local survivorship and invasion that is generally expected [e.g., Fridley *et al.* (2007)] and is observed for the end-Ordovician. One

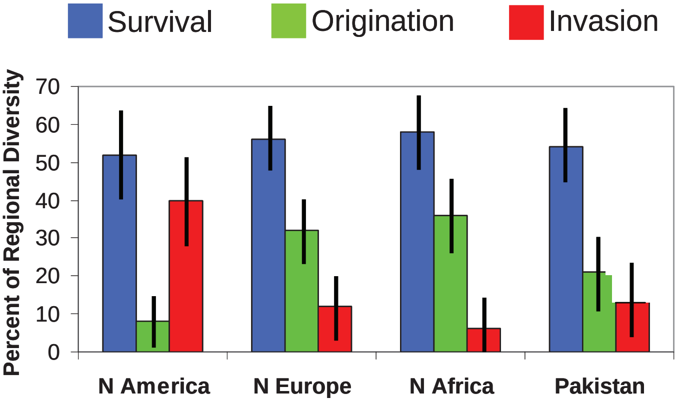

FIGURE 10.3 Regional variation in molluscan recovery dynamics after the K-T extinction. Four postextinction biotas are partitioned into their surviving, newly originating, or invading components. The Gulf and Atlantic Coastal Plain was subject to significantly more intense invasion than the other three regions (95% binomial confidence intervals). See Jablonski (1998) for details.

can speculate that this difference is attributable to the greater proximity of North America to the K-T impact site in Yucatan, but how does that proximity translate to great invasions without imposing exceptional extinction? Qualitative, rather than quantitative, losses might account for the greater invasibilty of North America, but this hypothesis has not been tested. Alternatively, the correlation between extinction intensity and subsequent invasion may begin to break down above some threshold extinction level. One clue may come from another spatial difference: the short-lived evolutionary burst of a few taxa in North America [“bloom taxa” of Hansen (1988)] that is evidently absent in northern Europe, North Africa, or Pakistan and India (Jablonski, 1998). North America’s bloom taxa and the invasion pulse are almost certainly linked, presumably indicating a more profound ecological and evolutionary disturbance in North America than elsewhere, but this needs to be examined more closely. Whatever the ultimate cause, the fossil record pinpoints a theoretically interesting but pragmatically disquieting gap in our understanding of the extinction–invasion relationship. Given the current acceleration of both processes, and the pressure to establish reserves for remaining biodiversity, this relationship deserves more attention.

EXTINCTION INFLUENCES SPATIAL DYNAMICS ACROSS LATITUDE

Extinctions apparently promote not only invasion but evolutionary diversification in the fossil record, the classic case being the impressive radiation of mammals after the demise of the (nonavian) dinosaurs and other marine and terrestrial vertebrates at the end of the Cretaceous [e.g., Alroy (1999, 2000) and Cifelli and Gordon (2007); for general discussions, see Erwin (2001) and Jablonski (2001, 2005, 2008)]. These macroevolutionary observations are often seen as two sides of the same coin, as they intersect nicely with ecological work on the potential for incumbency or priority effects to resist extinction or damp diversification (Jablonski, 2007, 2008). The three most prevalent explanations for both invasions and diversifications today and in the geologic past are (*i*) extinction or at least suppression of incumbents, already mentioned, (*ii*) superior competitive ability of the invaders, not least owing to their escape from their own competitors, predators, and pathogens when they enter a new area (Sax *et al.*, 2007) (although this may be a transient effect and therefore less likely to play a macroevolutionary role), and (*iii*) changing climatic and other environmental conditions, such as those that drove the extensive invasions and reshuffling of Pleistocene biotas.

One of the most pervasive spatial patterns of invasions, seemingly independent of mass extinction events, underlies the marine latitudinal diversity gradient, wherein morphologies, species, and higher taxa are richest in the tropics and decline toward the poles. Although the gradient has been known for a long time and is documented for many groups and regions, the processes underlying this pervasive biodiversity pattern remain poorly understood (Hillebrand, 2004; Mittelbach *et al.*, 2007). The "out of the tropics" model for the marine gradient has taxa preferentially originating in the tropics, and then expanding their latitudinal ranges over time without actually abandoning their tropical cradle (Jablonski *et al.*, 2006). The tropics are thus a diversity source, containing both young and old taxa, which accumulate to high richness. The poles are a diversity sink, mainly containing older taxa that have moved in from lower latitudes, and the temperate zones have intermediate richness and taxon ages, at least for the marine invertebrates where direct fossil evidence is available. If this model is generally true, then invasion is a basic factor in the latitudinal deployment of life on Earth.

The out-of-the-tropics model is strongly supported in the marine bivalve fossil record. For each of three time slices (Pleistocene, Pliocene, and late Miocene), roughly twice as many bivalve genera first occur in the tropics than in higher latitudes (Jablonski *et al.*, 2006). Because the extratropical fossil record is far better sampled than that of the tropics (Allison and Briggs, 1993; Jackson and Johnson, 2001; Bush and Bambach, 2004;

Jablonski *et al.*, 2006; Valentine *et al.*, 2006), the tropical values must be underestimates of their true origination rates, and the extratropical values must be overestimates. Further, most of the genera that first appeared in the tropics over the past 11 Myr have since spread to higher latitudes. This dynamic accounts for the striking inverse relation between diversity in a latitudinal bin and the median age of the genera in that bin: most of the geologically old genera at high latitudes also occur in the tropics, but the young genera are concentrated at low latitudes, decreasing the low-latitude median value significantly.

The number of taxa that expand out of the tropics is impressive, particularly given that these clades are invading new climate zones, traversing a gradient of increasing physical challenges for most taxa. Further, these extratropical expansions occurred in the face of progressive global refrigeration, culminating in the full-blown glacial cycles of the Pleistocene. However, while clades regularly left the tropics, few, if any, of the analyzed cohort have expanded above ≈50° north or south latitude. If the relative invasibility of the temperate and polar zones over the past 11 Myr was underlain by regional variation in background extinction intensity (**E**), we would expect, not the usual two-bin model, tropical **E** < extratropical **E**, or low-latitude **E** < polar **E** (Goldberg *et al.*, 2005; Jablonski *et al.*, 2006; Roy and Goldberg, 2007), or the monotonic latitudinal trend in extinction rates assumed by many others, but a hump-shaped pattern with an extinction maximum at midlatitudes.

A preliminary test of these alternatives did find a humped extinction pattern with latitude for Northern Hemisphere bivalve genera in the latest Cenozoic, with global plus regional extinction totaling ≈9% in the tropics, ≈20% in the temperate zone, and ≈12% in the Arctic (Valentine *et al.*, 2008). This result suggests that the temperate zones are invasible on geological timescales because they suffer the highest extinction rates, at least in global climate states approaching our own. Thus, even if climate does not directly set standing diversity, its fluctuations, which are greatest both in temperate latitudes today and during Pleistocene climate swings [e.g., Jansson and Dynesius (2002), Ravelo *et al.* (2004), and Lyle *et al.* (2008)], may set the pattern of extinction intensities. The data are not yet sufficient to study these dynamics in detail, but the relation between midlatitude thermal variability (which coincides with fluctuations in many additional factors) and extinction patterns clearly deserve further scrutiny. The poles are doubtless demanding places to live, but taxa evolve to cope with the challenges; Valentine and colleagues (Valentine, 1983; Valentine *et al.*, 2008) suggest they do this by becoming highly generalized trophically and argue that these broad niche dimensions are what tend to block invasions and allow them to weather glacial episodes subtidally, as they avoid seasonal extremes today. In any case, invasion resistance is apparently not a function of standing diversity alone, but of regional extinction rates, suggesting a significant role for incumbency [see also Vermeij (2005)]. The polar mollusks may ultimately have come out of the tropics as well, but if so this must have occurred before the 11-Myr window presently available (which would be consistent with the much older genus ages seen at the poles). The interplay of extinction, origination, and immigration is complex, and of course it need not be in a steady state.

Terrestrial animals may well follow a different dynamic (Hawkins *et al.*, 2007b; Weir and Schluter, 2007; Wiens, 2007a). Marine organisms can move down the continental shelf when ice forms at the surface, but terrestrial animals, plants, and fungi do not have that luxury when confronted with a kilometer-thick ice sheet. High-latitude extinction and recolonization are thus almost certainly more important factors on land. Whatever the spatial dynamic near the poles, however, the tropics appear to be a crucial reservoir for biodiversity, with a subset of low-latitude clades expanding out of the tropics over geological timescales. Although this pattern is most readily detected in the shallowest part of the geologic record, thus falling entirely within times away from the major mass extinctions, some evidence suggests that postextinction recoveries are also fueled by the tropics, on land (Kerp *et al.*, 2006) and in the oceans (Jablonski, 1998; Brayard *et al.*, 2006; Krug and Patzkowsky, 2007). The tropics thus appear to be key to the generation and maintenance of global biodiversity across a wide range of boundary conditions.

INTEGRATING PALEONTOLOGICAL AND NEONTOLOGICAL PERSPECTIVES

I have touched on four spatial aspects of ancient extinctions that should be integrated with theoretical and applied approaches to the present-day biota. The fossil record amply demonstrates that the spatial fabric of extinction has profoundly shaped the biosphere. First, broad geographic range probably always buffers clades from extinction, but it becomes most important and clear-cut as the suite of other factors that enhance species and genus survival during normal times become ineffective. It is not yet clear whether the selectivity regime changes steadily with increasing extinction intensity or as a step function (Jablonski, 2005). More intense extinctions may tend to be less selective, which might explain the failure of intrinsic factors to predict extinction risk in the some of the most heavily stressed elements of the modern biota, such as freshwater fishes, amphibians, and Australian marsupials (Duncan and Lockwood, 2001; Fisher *et al.*, 2003).

This shift to a strong spatial component in survivorship during major extinction events greatly increases the likelihood of hitchhiking effects.

Organismic traits can rise or fall according to the strength of their linkage to broad geographic range or other factors promoting survivorship through those bottlenecks, lending a highly stochastic element to the expansion or demise of individual adaptations or clades. Thinking about the present day, these linkages are unlikely to promote factors beneficial to, or even desirable for, humans or the ecosystems they hope to conserve (see Jackson, Chapter 1, this volume). Given that narrow-ranging genera cannot have wide-ranging species, the net effect must be to deplete specialists in favor of weedy generalists, but this pattern can be ameliorated by survival of clades whose broad ranges arise from the far-flung deployment of individually localized species.

Second, the fossil record is rich in regional extinction events of intermediate intensities, and these can provide insights into present-day biodiversity issues. For example, the Cenozoic history of today's biodiversity hotspots and coldspots (relative to expectations for their latitudes, for example) may help to predict the potential of these regions to accommodate further diversification, or alternatively to be subject to biotic invasions.

Third, the rules of successful recovery are poorly known, but are important for our understanding of both the larger outlines of the history of life and the future of modern diversity. The inordinate production of evolutionary novelties during recoveries suggests that postextinction dynamics do not simply involve an immediate return to business as usual. At the same time the spatial heterogeneity of recoveries, with significant invasions driving some of the regional patterns, requires a more careful look at the dynamics if we want to avoid biotic homogenization even after the reduction of the pressures on the modern biota. This could be another highly fruitful area at the intersection of paleontology and conservation biology.

Fourth, invasion has always been an evolutionary fact of life (Vermeij, 2005), even across biogeographic barriers and against climate gradients. The out-of-the-tropics model suggests an evolutionary approach to modeling biotic responses to future climate changes and attests to the evolutionary consequences of the stresses on tropical biotas today. If the tropics are the engine of global biodiversity, then driving tropical populations into extinction will have a global effect, by cutting off the primary source of new taxa for all latitudes. Further, if invasibility is more closely tied to extinction than to diversity *per se*, then there is the possibility of a reversal of the diversity flow, increasing the influx of invaders from higher latitudes. A tropical diversity crisis, now or in the geologic past, has profound long-term evolutionary consequences at a truly global scale.

Simply comparing the magnitude of the extinction occurring today, which is undoubtedly severe, with ancient intensities is not the most fruitful way to draw on the insights of the fossil record, or catalyze integrative research. A better approach might be to recognize that present-day extinctions have many drivers, and then to test for common patterns of selectivity on that basis: partitioning present-day extinction mechanisms should permit a clearer application of insights from the fossil record. Extinction selectivity probably does vary with driving mechanism to some extent. In birds, for example, habitat loss preferentially removes specialized and small-bodied taxa (but does not select on generation time), whereas exploitation and introduced predators preferentially remove large-bodied and long-lived taxa (Owens and Bennett, 2000). Such systematic variations in selectivity help explain the apparent contradictions in and among analyses of present-day extinction risk [e.g., Purvis *et al.* (2000b) and Fréville *et al.* (2007)], and similar arguments can be made for differences among ancient extinctions as well. As several authors have noted, extinction drivers have probably compounded over human history, with exploitation perhaps the most important in early phases, species invasions rising in frequency with the era of European exploration, and finally habitat alteration on a global scale accelerating with increased human population pressure, pollution, and climate change [e.g., Purvis *et al.* (2000b) and Jackson *et al.* (2001)].

Many paleontological perturbations are probably most analogous to present-day habitat loss and could be explored in comparative fashion on that basis. Others will more closely correspond to the introduction of enemies, as when provinces collide or novel predation mechanisms evolve (see Barnosky, Chapter 12, this volume). The particular combination of pressures seen today may be unique, just as they may have been for the K-T or end-Permian events. For example, today the ordinary biotic response to climate change (range translocation) is disallowed or at least severely curtailed over much of the planet owing to occupation or conversion of suitable habitat or migration corridors by humans and their artifacts. The unique combination of forces behind each major extinction puts a premium on focusing on first principles rather than extinction-specific patterns, underscoring the need for integrative research. It also underscores the need to take a hard look at the roles of incumbency and hitchhiking effects, to separate large-scale artifacts or byproducts from the underlying drivers. Extinction thresholds presumably exist for today's biota, beyond which whole systems collapse and most selectivity factors drop out, as seen for major events of the geologic past. Identifying such thresholds among environments, clades, and regions using fossil data, as another basis for avoiding them in the future, would be a valuable undertaking.

More generally, spatially explicit approaches to the fossil record have great potential for new insights into diversity dynamics, not just in the geologic past, but in the present day as well. The integration of paleontological and neontological insights takes on special urgency with the acceleration of extinction rates in the modern world, and the incorporation of the spatial dimension offers a powerful vehicle for that integration.

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11

Dynamics of Origination and Extinction in the Marine Fossil Record

JOHN ALROY

The discipline-wide effort to database the fossil record at the occurrence level has made it possible to estimate marine invertebrate extinction and origination rates with much greater accuracy. The new data show that two biotic mechanisms have hastened recoveries from mass extinctions and confined diversity to a relatively narrow range over the past 500 million years (Myr). First, a drop in diversity of any size correlates with low extinction rates immediately afterward, so much so that extinction would almost come to a halt if diversity dropped by 90%. Second, very high extinction rates are followed by equally high origination rates. The two relationships predict that the rebound from the current mass extinction will take at least 10 Myr, and perhaps 40 Myr if it rivals the Permo-Triassic catastrophe. Regardless, any large event will result in a dramatic ecological and taxonomic restructuring of the biosphere. The data also confirm that extinction and origination rates both declined through the Phanerozoic and that several extinctions in addition to the Permo-Triassic event were particularly severe. However, the trend may be driven by taxonomic biases and the rates vary in accord with a simple lognormal distribution, so there is no sharp distinction between background and mass extinctions. Furthermore, the lack of any significant autocorrelation in the data is inconsistent with macroevolutionary theories of periodicity or self-organized criticality.

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Decades of literature on large-scale taxonomic diversification and extinction patterns have hinged on compilations that record little more than first and last appearances of families or genera. Key examples include Sepkoski's compendia of marine families (Sepkoski, 1984) and genera (Sepkoski, 1996) and the Fossil Record 2 database of marine and continental families (Benton, 1993). Numerous patterns of widespread scientific and public interest have been identified on the basis of the older compilations, such as the identity of the five largest mass extinctions (Raup and Sepkoski, 1982; Raup, 1986), a gradual decline of extinction rates throughout the entire Phanerozoic (Raup and Sepkoski, 1982), and possible cycles in extinction rates (Raup and Sepkoski, 1984). A complete reevaluation of these hypotheses is now made possible by the maturation of the Paleobiology Database, a relational, web-based, and much more detailed resource created by and for the paleontological community (Alroy *et al.*, 2001).

Arguably, the most enduring and biologically important question these data can answer is whether global biodiversity is saturated (Sepkoski, 1978, 1979, 1984). If so, then ecological interactions, such as competition and predation, must control rates of speciation and extinction (MacArthur, 1969; Rosenzweig, 1975; Walker and Valentine, 1984). Speciation rates must be lower or extinction rates must be higher than they would be without these interactions. Diversity curves should increase logistically as they approach the saturation point (Sepkoski, 1978) instead of exponentially (Benton, 1995). Increases in the diversity of major taxonomic groups should be balanced by decreases in the diversity of other groups (Sepkoski, 1979). Most importantly, any recovery from a mass extinction, such as the current one, should eventually bring diversity back to the saturation point. Of course, the recovery will be rapid only in geological terms, the saturation point may change, and the extinction may fundamentally reorganize the global biota both taxonomically and ecologically, as seen in the wake of major perturbations, such as the end-Permian crisis (Erwin, 2001).

Past predictions about recovery have been hampered by limited direct evidence for saturation in the fossil record. Sepkoski (1978, 1979, 1984) did argue in detail that turnover rates have constrained the global diversity of all marine animals over the entire Phanerozoic. Some studies of particular taxonomic groups over specific parts of the Phanerozoic also suggested density-dependent dynamics (Mark and Flessa, 1977; Wagner, 1995; Alroy, 1996, 1998; Connolly and Miller, 2002). However, both earlier (Flessa and Levinton, 1975) and later (Benton, 1995) workers argued that Phanerozoic diversity was not constrained. Even though this view is very inconsistent with such well-documented patterns as rapid rebounds from mass extinctions (Kirchner and Weil, 2000b; Erwin, 2001; Foote, 2003), a basic logistic model assuming a single equilibrium point (Sepkoski, 1978) failed to explain in a simple way why diversity appeared to increase exponentially in the Cretaceous and Cenozoic, toward the end of the Phanerozoic (Sepkoski, 1984). Instead, a model with multiple equilibria was invoked (Sepkoski, 1979, 1984).

More recently, evidence has accumulated that the late Phanerozoic radiation is actually a combined artifact of increased sampling intensity and a related effect called the Pull of the Recent (Foote, 2000a; Alroy *et al.*, 2001, 2008; Peters and Foote, 2001). Thus, the question of diversity equilibrium has been reopened. The strong statistical patterns reported here show that diversity does not increase exponentially without constraints and therefore make it possible to predict the rebound from the current mass extinction in strict quantitative terms. First, however, a series of other major hypotheses concerning mass extinctions and diversity dynamics need to be addressed.

Pulsed Turnover Rates

Based on Sepkoski's classic family- and genus-level data (Sepkoski, 1984, 1996), it has been suggested that turnover comes in large pulses that coincide with interval boundaries (Foote, 1994b, 2005). If true, this result has the profound implication that even background turnover is largely forced either by perturbations, such as eruptions, sea level and climate changes, and bolide impacts (Raup, 1992), or by episodic ecological interactions, such as cascading extinctions (Plotnick and McKinney, 1993). If turnover is not coupled with boundaries, an alternative hypothesis is that background extinction is effectively stochastic and results from the never-ending process of competition over a fixed or slowly changing resource base, i.e., the Red Queen hypothesis (Van Valen, 1973).

The pulsed turnover hypothesis implies that per-million year (Myr) rates will correlate inversely with interval lengths because the assumption that turnover is continuous is violated (Raup and Sepkoski, 1984). There is such a relationship for per-Myr extinction rates (Spearman rank-order correlation $\rho = -0.409$, $P < 0.005$). However, the same correlation does not exist in the unstandardized rates [$\rho = -0.021$, not significant (n.s.)] and is not significantly different from a distribution generated by bootstrapping (i.e., correlating raw rates with ratios of themselves to randomly drawn bin lengths). Thus, the relationship can be explained as resulting from random variation in the bin lengths because of random errors in the underlying timescale. The same pattern is seen with originations, i.e., first appearances of genera. Origination rates correlate negatively with bin length if they are standardized ($\rho = -0.408$, $P = 0.005$) but otherwise do not ($\rho = 0.155$, n.s.). These results, however, do not particularly endorse the Red Queen hypothesis because rates are still quite variable, as discussed below.

On balance, it is most parsimonious to infer that, although turnover may or may not be pulsed, interval boundaries do not coincide consistently with pulses, so continuous-time rates are more realistic than turnover proportions. These rates also have the advantage of removing the upper bound present in proportions, which can cause analytical artifacts. The continuous rates are not standardized for bin length in subsequent analyses because of the timescale's relative homogeneity and the suggestion that doing so would bias them. For the current dataset, this technical problem is most likely moot, because there is no trend through time in bin length ($\rho = 0.168$, n.s.), and the standard deviation of logged bin lengths is modest (0.348).

Phanerozoic Decline in Extinction Rates

Again based largely on Sepkoski's data, it has long been believed that there has been a decline through the Phanerozoic in both extinction rates (Raup and Sepkoski, 1982) and origination rates (Gilinsky and Bambach, 1987). These observed declines are robust to the choice of rate metrics (Foote, 1994b). Indeed, the new data clearly support a decline in both kinds of rates (extinction vs. time: $\rho = 0.547$, $P < 0.001$; origination vs. time: $\rho = 0.533$, $P < 0.001$). The patterns are influenced by extremely high values at the beginning of the time series that represent the Cambrian and earliest Ordovician (Fig. 11.1). However, removing these points does not greatly weaken the trends (extinction: $\rho = 0.446$, $P = 0.003$; origination: $\rho = 0.465$, $P = 0.002$). It is noteworthy that the correlations still appear even though the earlier studies (Raup and Sepkoski, 1982; Gilinsky and Bambach, 1987; Gilinsky, 1994) used finer timescales and therefore had greater statistical power. They also did not correct for sampling biases that would favor finding such a pattern.

To quantify the steepness of the declines, it is appropriate to perform a linear regression after log-transforming the turnover rates (Quinn, 1983; Foote, 1994), which is necessary because they are skewed and bounded by zero. For extinction and origination after the earliest Ordovician, the respective regression slopes are 0.201% and 0.158% per Myr, and the intercepts at 0 Ma are 0.218 and 0.282. Sepkoski's data imply much steeper slopes and predict much lower extinction rates for the Neogene (Peters, 2006), which is expected because the data are influenced by the Pull of the Recent.

The drop in rates could be explained in at least four ways. First, a trend might be created by sampling biases or an increase through the Phanerozoic in the average durations of sampling bins (Pease, 1992). The former problem has been fully resolved by sampling standardization of the data and by the use of rate equations that are robust to edge effects

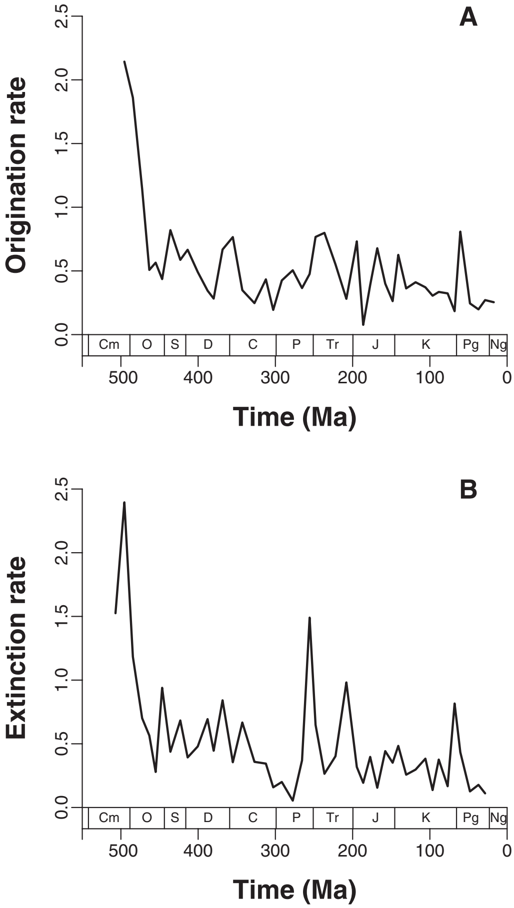

FIGURE 11.1 Per-interval instantaneous origination rates (*A*) and extinction rates (*B*) of marine invertebrate genera over the Phanerozoic. Data are binned into 48 intervals averaging 11.0 Myr in duration.

such as the Pull of the Recent. The latter problem has been resolved by careful lumping of stages to produce bins of approximately equal length, as mentioned above.

Second, the trends could reflect a handoff between major groups that had coupled logistic dynamics (Sepkoski, 1984). Groups that were dominant early on might have had higher intrinsic turnover rates but lower carrying capacities, leading eventually to their replacement by slowly radiating competitors. Here, these groups would be the three "evolutionary faunas" (Sepkoski, 1981). Evidence is lacking for dynamically distinct but interacting groups of taxa based on actual turnover rates in Sepkoski's own genus-level compendium (Alroy, 2004), so the evolutionary fauna hypothesis is not relevant here and is most likely useful only to summarize coincidences between diversity trends (Sepkoski, 1981) and onshore-offshore patterns (Sepkoski and Miller, 1985).

Third, individual orders with high turnover rates might have randomly gone extinct by the mid-Paleozoic simply because of their volatile dynamics, leaving only the groups with low turnover rates (Gilinsky, 1994). Neither this hypothesis nor the preceding one can be tested directly by using the new data without separating the major taxonomic groups, but at least the volatility model is supported by analyses of Sepkoski's data (Gilinsky, 1994).

Finally, higher taxa such as families may tend to accumulate more species through time, reducing their chance of extinction (Flessa and Jablonski, 1985). A similar argument holds for origination. Raup (1976) provided estimated species totals for the Cenozoic and for each Paleozoic and Mesozoic period that can be compared with genus totals extracted from Sepkoski's (1984) compendium. Although the ratios are probably too low, because the species counts are two decades older, there is a striking increase from 2.6, 2.7, and 2.1 in the Cambrian, Ordovician, and Silurian, to 5.4 and 7.8 in the Cretaceous and Cenozoic, with all other periods falling in between. More detailed analyses are called for, but the difference is so large that it could easily explain the trend.

Big Five Mass Extinctions

The apparent existence of five major peaks in extinction rates is another key finding in the literature on Phanerozoic marine diversity (Raup and Sepkoski, 1982; Raup, 1986). The Big Five theory is so widespread that it has given rise to the popular term "sixth extinction" in relation to the current crisis (Leakey and Lewin, 1995; Glavin, 2007). These peaks were first recognized because they rose beyond the parametric 95% confidence interval around a linear regression that described the Phanerozoic decline in extinction rates (Raup and Sepkoski, 1982). The Big Five also appear to be present in a separate compilation of marine family-level data (Benton, 1995), and at least the Permo-Triassic and Triassic–Jurassic events register as well in data on continental organisms (Benton, 1995).

However, there were numerous problems with the original analysis, including failure to log the data (Quinn, 1983) and the use of per-Myr but not per-taxon rates. Indeed, the original data (Raup and Sepkoski, 1982) did not particularly support the existence of two mass extinctions now widely discussed, the late Devonian and end-Triassic (Raup and Sepkoski, 1983). Although the five greatest proportional drops in diversity in Sepkoski's later genus-level data (Sepkoski, 1996) do match the conventional Big Five extinctions, the late Devonian and end-Triassic drops apparently are driven more by origination deficits than by high extinction rates [Bambach *et al.* (2004); however, in the new data, the latter decline is a legitimate mass extinction]. Furthermore, the end-Ordovician peak in Sepkoski's family-level data has been called into question because its appearance depends on the rate metric being used (Foote, 1994b).

Finally, the very idea that the Big Five represent anything but the upper end of a continuous range of variation has been questioned almost from the start (Raup, 1986; Wang, 2003). Although there are other good ways to test for outliers in rate distributions (Wang, 2003), it is sufficient to compare the rates with what is expected of the same number of observations drawn from a best-fit normal distribution. The rates first need to be detrended by taking residuals of the regression line that was earlier fit to the logged data. The detrended distributions (Fig. 11.2) are in fact indistinguishable from the lognormal based either on a Kolmogorov–Smirnov test (extinction: $D = 0.0888$, n.s.; origination: $D = 0.0883$, n.s.) or a Shapiro–Wilk test (extinction: $W = 0.9657$, n.s.; origination: $W = 0.9548$, n.s.). Additionally, although extinction rates are much more variable than origination rates in Sepkoski's datasets (Foote, 1994b), here the standard deviations of the detrended rates are very similar (extinction: 0.613; origination: 0.466) and the distributions are statistically indistinguishable ($D = 0.2215$, n.s.). Thus, not only are there no distinct classes of major origination or mass extinction events, but there is minimal evidence that extinction rates are more volatile than origination rates.

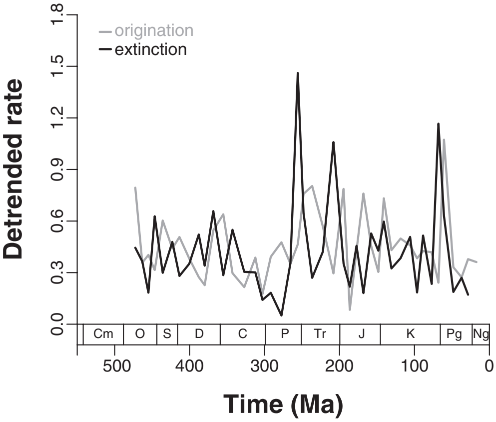

FIGURE 11.2 Origination rates and extinction rates after being detrended by using exponential functions.

These results do not challenge the idea that true mass extinctions impose different rules of survivorship relating to factors such as geographic range size (Jablonski, 1986a), because the rules could well vary with extinction intensity even if intensity *per se* is largely random. They also do not challenge the idea that we are in the midst of a mass extinction on par with all but a handful of such events over the last half billion years (Myers and Knoll, 2001).

Furthermore, the data confirm that three of the Big Five extinctions (the Permo-Triassic, end-Triassic, and Cretaceous-Tertiary) are the three largest of the Phanerozoic, if only after detrending the rates (Fig. 11.2). These events stand out very clearly if the data are not log-transformed. Additionally, although the Paleozoic data show very little variability, one of the two largest events within the Paleozoic is indeed the end-Ordovician extinction. The other comes at the Devonian–Carboniferous boundary, immediately after the late Devonian event typically ranked in the Big Five. As mentioned, the late Devonian episode's importance already has been called into question (Raup and Sepkoski, 1983; Foote, 1994b; Bambach *et al.*, 2004). In summary, it is a matter of taste whether to speak of the Big Five, the Big Three, or just the Big One, but one way or another major mass extinctions are truly very rare.

Periodicity and Self-Organized Criticality

The hypothesis that mass extinctions show an ≈26-Myr cycle of periodicity (Raup and Sepkoski, 1984) has arguably been the most debated hypothesis by paleontologists over the last quarter century. A host of potential mechanisms for periodicity have been offered, such as impacts driven by astrophysical factors (Raup and Sepkoski, 1984) or the lag time needed either to accumulate species vulnerable to mass extinction (Stanley, 1990) or to build networks of ecological interactions that can collapse if even slightly perturbed (Plotnick and McKinney, 1993).

Qualitatively, it is hard to discern some of the extinction rate peaks that should fall in the periodic pattern (Benton, 1995). Quantitatively, extinction rates in the Fossil Record 2 family data (Benton, 1993) and Sepkoski's family and genus data (Sepkoski, 1984, 1996) are not correlated with themselves at any time lag (Kirchner and Weil, 2000a), which is a necessary condition for periodicity to hold. That said, analyses of origination rates in all three datasets (Kirchner and Weil, 2000a; Kirchner, 2002) suggest short-term autocorrelation. However, the current dataset shows no autocorrelation in either kind of rate, and a standard spectral analysis also suggests purely random variation through the time series (i.e., white noise).

The idea that mass extinctions may result from small perturbations of complex ecosystems (Plotnick and McKinney, 1993) has been expanded to argue that food webs naturally evolve to a state of self-organized criticality that creates the extinction cascades, even in the absence of perturbations (Sneppen *et al.*, 1995; Solé *et al.*, 1997). Criticality models make direct predictions about patterns of autocorrelation in time series (Solé *et al.*, 1996, 1997). However, results suggesting criticality in several major paleontological datasets (Solé *et al.*, 1997) were quickly rebutted as statistical artifacts that resulted from interpolating turnover rates to create numerous evenly spaced intervals (Kirchner and Weil, 1998; Newman and Eble, 1999). With the new data, the slope of the spectral density/frequency relationship is far from the value predicted by criticality; it is effectively zero. Thus, self-organized criticality can be dismissed as a plausible explanation of extinction rates.

Finally, it also has been suggested that diversity itself is cyclical with a period of ≈62 Myr, regardless of turnover rates (Rohde and Muller, 2005). This pattern was again compromised by the use of Sepkoski's unstandardized data, and it had serious plausibility problems: Although extinction rates do not show long-range periodicity, most of the predicted peaks only appeared to be peaks because they were followed by the nominal Big Five extinctions (e.g., Raup and Sepkoski, 1982; Kirchner and Weil, 2000a). No distinct peaks were seen within the Cretaceous and Cenozoic (Rohde and Muller, 2005), and there is also no evidence in the current dataset (Alroy *et al.*, 2008) for the predicted early Cambrian peak, or for a valley separating the supposed late Ordovician and Devonian peaks.

The current diversity curve does show a weak cycle after removing its U-shaped trend by taking residuals of a quadratic function fitted to the logged data. However, the cycle has a period somewhat longer than 62 Myr, and the pattern is driven by clearly coincidental matches between two peaks and two valleys. The spectral density data also suggest periodicity. However, the steep falloff at medium frequencies is driven by these weak matches and consistent with either a power law or exponential function, so it is not evidence of self-organized criticality (Newman and Eble, 1999).

EQUILIBRIAL DYNAMICS

Density Dependence

The lack of periodicity in turnover rates does not imply that these rates are random and therefore does not imply that the diversity curve evolves randomly. The reason is that at least three causal relationships might regulate diversity and turnover while not producing marked autocorrelation. First, origination rates may correlate negatively with preceding diversity levels (Rosenzweig, 1975; Sepkoski, 1978). An equilibrium will result, because high diversity will lead to an origination deficit, low diversity will lead to a burst of origination, and intermediate diversity will lead to a balance of origination and extinction. Second, diversity and subsequent extinction rates may correlate positively, producing an equilibrium for similar reasons (Rosenzweig, 1975; Sepkoski, 1978). Both relationships have been found in Sepkoski's family- and genus-level data (Foote, 1994b, 2000b). Third, origination and extinction may be positively correlated (Webb, 1969; Flessa and Levinton, 1975; Mark and Flessa, 1977; Alroy, 1996, 1998). Such a correlation will greatly slow the net movement of the diversity curve and has been observed in Sepkoski's data (Kirchner and Weil, 2000b; Foote, 2003).

These hypotheses can be tested by computing simple correlations among the turnover rates (λ and μ) and diversity (N_s). There are no strong correlations in the raw data between either extinction or origination and diversity in the immediately preceding, current, or succeeding bins. However, the picture changes after detrending the turnover rates (Fig. 11.2) and diversity curve; as it should, detrending markedly reduces the correlation between neighboring diversity values, with $\rho = 0.769$, $P < 0.001$ instead of $\rho = 0.464$, $P = 0.002$.

Now there is a correlation between past origination and current diversity ($\rho = 0.327$, $P = 0.035$). However, this weak relationship may be influenced by analytical biases, and there is no correlation between past extinction and diversity ($\rho = -0.214$, n.s.). Of more interest is a stronger match (Fig. 11.3*A*) between current diversity and immediately following extinction ($\rho = 0.439$, $P = 0.004$) but not origination ($\rho = -0.039$, n.s.). The diversity/extinction relationship is unlikely to result from a commonly encountered bias called regression to the mean (Freckleton *et al.*, 2006). Concurrent diversity and extinction also correlate with the predicted positive sign, if not significantly ($\rho = 0.243$, n.s.), and likewise concurrent origination is not predictable ($\rho = 0.223$, n.s.). Finally, there is a match (Fig. 11.3*B*) between past extinction and future origination ($\rho = 0.337$, $P = 0.029$) but not the other way around ($\rho = 0.016$, n.s.), with independence of concurrent rates ($\rho = 0.111$, n.s.).

The two strong relationships are crucial, because they are responsible for the suggested equilibrium: high diversity will be brought down by high extinction rates, and large extinctions will be compensated by high origination rates. After splitting the data at the Permo-Triassic boundary, sample sizes are too small to establish significance, but consistent patterns in both relationships are still seen (Fig. 11.3). Furthermore, the predicted relationships hold up after removing the outlying end-Permian extinction rate (diversity and future extinction: $\rho = 0.396$, one-tailed $P = 0.006$; extinction and future origination: $\rho = 0.291$, one-tailed $P = 0.033$).

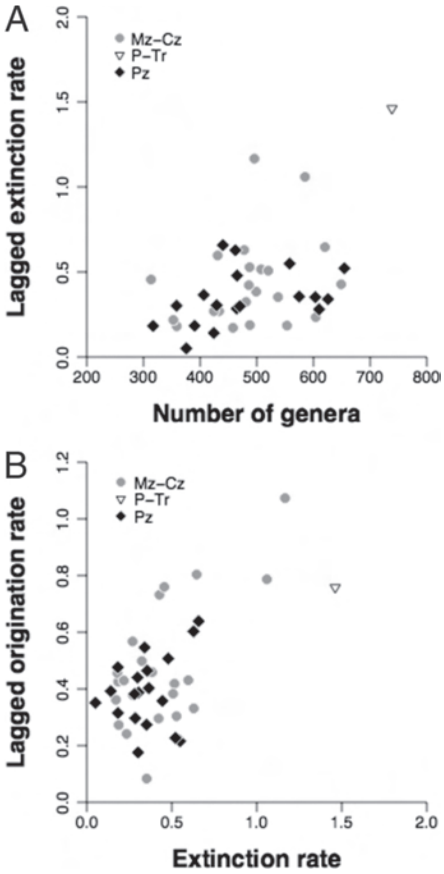

FIGURE 11.3 Key relationships between variables that govern marine invertebrate diversity dynamics on the Phanerozoic scale. Paleozoic points (black diamonds) and Meso-Cenozoic points (gray circles) show the same patterns in each case, and the values including the Permo-Triassic mass extinction (triangle) are consistent with the trends. (*A*) Correlation between diversity in one interval and extinction rates in the next interval. (*B*) Correlation between extinction rates in one interval and origination rates in the next.

Causal Model

Obviously, origination rates cannot respond directly to a memory of extinction rates in the far past. Ghosts do not speak, so their empty niches must somehow beckon. The problem is how to reproduce such a process without making origination density-dependent, which cannot be accomplished in any way with conventional logistic models (Sepkoski, 1978), simple lattice-based niche incumbency models (Walker and Valentine, 1984), or percolation models in which all empty cells are filled immediately by origination (Plotnick and McKinney, 1993).

The only way I have been able to predict all of the key relationships is with a cell model in which the number of cells is effectively infinite, underlying origination rates follow a random walk, new species can only fall in unoccupied neighboring cells, and underlying extinction rates are some joint function of white noise and the overall current number of species. Any other combination of factors seems to either create density dependence of origination rates or remove one or both of the two key correlations.

In plain English, this model depends on direct competition to regulate both speciation and extinction. The former process is basically niche incumbency (Walker and Valentine, 1984) with limited rates of adaptation, local interactions, and no fixed number of niches, and the latter process is a routine logistic function (Sepkoski, 1978). Competition is the opposite of the interdependency built into percolation and self-organization criticality models (Plotnick and McKinney, 1993; Sneppen *et al.*, 1995; Solé and Bascompte, 1996; Solé *et al.*, 1996). Meanwhile, the assumption of slowly changing origination rates is consistent with slow sorting of large clades that have distinctive turnover rates (Gilinsky, 1994), whereas adding a high-frequency random component to extinction rates is consistent with evidence that the Permo-Triassic and Cretaceous-Tertiary mass extinctions involved unpredictable physical forcing mechanisms (Erwin, 2001). The overall scenario may seem restrictively complex, but at least complexity maximizes testability. Perhaps a simpler theory can be found that predicts the correlations, but even this moderately rich one fails to cleanly predict the apparent nonlinearity of the origination rate response to mass extinction (Fig. 11.3*B*).

Previous Studies

Put together, these results combine to make a plausible and straightforward scenario. First, a major drop in diversity for any reason will be followed by a significant recovery due to the near-absence of extinction. Extinction rates may continue to be low for a second 11.0-Myr interval after the immediate recovery. Second, if the drop was due to a large extinction pulse and not merely an unfavorable balance of origination and extinction, then speciation rates will increase dramatically.

Earlier researchers have argued for entirely different models. For example, autocorrelation in Sepkoski's origination rates (Kirchner and Weil, 2000a), apparently greater variation in extinction than origination (Kirchner, 2002), and, most importantly, a lagged correlation between extinction and subsequent origination in Sepkoski's family- and genus-level data (Kirchner and Weil, 2000b) have been used to construct a theory that diversity is slow to rebound from extinction because time is required to reconstruct ecological niches that might be filled.

There are numerous problems with Sepkoski's data that call these results into question: the lack of any sampling standardization, the unavoidable backward smearing of extinction rates and forward smearing of origination events that results from using simple range data (Foote, 2003), and the oversplitting of the timescale into 106 intervals (as opposed to 48 in this study). Not surprisingly, the first two hypothesized patterns do not exist in the current dataset: Origination rates lack any significant autocorrelation and are not much less variable than extinction rates.

An extinction-origination correlation is indeed present, but the pattern is different from expected under the hypothesis that niches need to be reconstructed. First, very high origination rates come immediately after what are clearly rapid mass extinctions (Fig. 11.3*B*), not a full temporal bin later (Kirchner and Weil, 2000b). Second, only the largest extinctions seem to boost immediately subsequent origination. If Kirchner and Weil (Kirchner and Weil, 2000a,b; Kirchner, 2002) are right that niches need to be reconstructed, then recoveries should be slower and not faster after a large extinction, because the relevant ecological interactions are more highly disrupted. Thus, if niches are relevant, then speciation in the wake of mass extinctions is most likely fostered by the lack of competition for existing niches instead of being delayed by the elimination of old niches that need to be reconstructed.

Meanwhile, some support for a diversity/extinction relationship has been found in Sepkoski's datasets (Sepkoski, 1984; Foote, 2000b). However, these results did not involve lagging, and Sepkoski's genus-level data provide mixed support for density dependence in both kinds of rates instead of just extinction rates (Foote, 2000b). The consistency of the diversity-extinction relationship through the Phanerozoic (Fig. 11.3*A*) also is at odds with earlier analyses suggesting fundamental changes across the Permo-Triassic in ecology (Erwin, 2001; Wagner *et al.*, 2006) and especially diversity dynamics (Foote, 2000b). The latter study found correlations between changes in diversity and changes in rates. The motivation for differencing the rates was to avoid biases and autocorrelation (Foote, 2000b), but the current dataset uses rates with low bias that lack autocorrelation, so differencing is moot. Again, biases related to sampling, counting, and rate equations are likely to be a problem in all of the earlier studies.

Recovery Predictions

The two major correlational relationships (Fig. 11.3) are well constrained over a realistic range of diversity and turnover levels, making it reasonable to offer specific predictions about the recovery from the mass extinction that is clearly underway (Myers and Knoll, 2001; Wake, 2008).

First, however, the relationships need to be modeled as accurately as possible, which requires transforming the data appropriately and then fitting linear regression functions.

The detrended diversity curve falls in such a narrow range that it is normally distributed on either a linear, log, or square root scale according to a Shapiro–Wilk test. However, logging diversity data is intuitive because diversification is a multiplicative process. For the detrended extinction rates, the raw data are far too skewed to be normal ($P < 0.001$), and taking square roots does not really help ($P = 0.030$). However, logging does render them normal, and the parametric correlation r between log diversity and log future extinction (0.462) is much the same as the rank-order correlation ρ (0.439). Like extinction rates, origination rates are too skewed to be normal ($P = 0.011$). Technically, logging does normalize them ($P = 0.090$), but the square root transform does a slightly better job ($P = 0.455$).

For the data starting after the earliest Ordovician, the median extinction rate is 0.380, and the diversity:extinction regression line is so strong that it implies a near-zero rate when diversity is 1 (i.e., the intrinsic rate). For example, at diversity levels 50, 90, and 99% below the median, the predicted extinction rates are 0.133, 0.014, and 0.0005, respectively. Thus, there would be hardly any extinction if not for major environmental perturbations and the ecological interactions that generate density dependence. Of course, that does not mean the rates are entirely predictable; it simply means that if abundant data were to extend all the way down to a diversity level of 1, we would find that density dependence explained a large majority of the variance. Indeed, the residual variance of the actual regression (Fig. 11.3*A*) is substantial and, therefore, likely to be real.

The second step is to model origination as a function of past extinction. However, origination rates cannot be predicted solely from the contemporary extinction rates produced in the first step without producing pathological results, because the initially low extinction rates would imply low, not high, origination rates. Instead, the extinction rates put into the equation need to reflect the entire loss of diversity relative to the starting point. The solution is to add the log ratio of preextinction diversity to current diversity to the predicted rate.

Put together, the two functions paint a grim picture (Fig. 11.4). A mass extinction on the scale of the Permo-Triassic event would probably leave diversity still 20% below its equilibrium level after ≈40 Myr, which is nearly as long as a typical geological period. Indeed, a comparable recovery from even the weakest modeled extinction is expected to take ≈10 Myr, and a 90% recovery would take ≈20 Myr. The worst-case scenario is not unthinkable for marine invertebrates: any increase in global atmospheric CO_2 by >500 ppm would cause coral reef ecosystems to collapse (Hoegh-Guldberg *et al.*, 2007), and, putting everything else aside, biotic

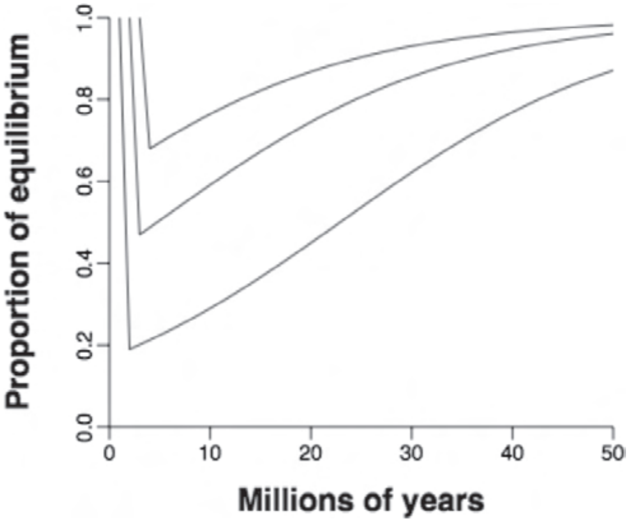

FIGURE 11.4 Predicted recoveries from mass extinctions modeled on the global Permo-Triassic and Cretaceous-Tertiary events (81% and 53% losses, respectively) and the early Pleistocene extinction in the Caribbean (32% loss) (Todd *et al.*, 2002).

homogenization through species introductions could cause up to a 58% mass extinction (McKinney, 1998).

Origination rates do vary significantly from one 11.0-Myr bin to the next (Figs. 11.1*A* and 11.2*A*), so stochastically achieved high rates in a few bins could push diversity to its equilibrium much faster. Indeed, full recoveries seem to have taken place within the span of one bin after the end-Ordovician and Cretaceous-Tertiary mass extinctions (Alroy *et al.*, 2008). Nonetheless, a minimum 10-Myr recovery time is consistent with qualitative assessments of the pace of recovery in the geological record (Erwin, 2001).

DISCUSSION

The tests reported here show that diversity is constrained and provide direct evidence of the major mechanism. When diversity is high for any reason, extinction rates rise both in the same interval and the immediately following ones. When diversity is low because of a preceding major mass extinction, origination rates rise. Because the relationships are temporally offset, the direction of each causal relationship is clear. Extinction seems to be forced by some aspect of rising biodiversity, but the reverse is not true. Meanwhile, origination seems to be spurred by the emptying of many niches at once but origination bursts do not cause those niches to be emptied rapidly later on.

The only clear-cut processes that could create such responses are ecological interactions, such as competition and predation, that affect the overall probability of speciation and extinction. Presumably, these interactions influence attributes of species, such as population size, population density, and geographic range size, that are not properties of individual organisms regardless of whether one wants to call them emergent or aggregate (Jablonski, 2000). Density dependence therefore may intensify differential reproduction of species based on traits that are likely to be heritable between species, again, regardless of whether one wishes to call this process species selection or sorting.

None of these results imply that density dependence is the sole governing mechanism of diversification. Quite the contrary, there is much variation left in both the diversity data and the turnover rates that might be explained by other factors, such as short-term perturbations [e.g., bolide impacts (Raup, 1992)] and longer-term changes in the environment [e.g., sea level (Peters and Foote, 2001; Peters, 2006)]. The analyses also only pertain to genera common and widespread enough to be recovered in the fossil record, and the diversity of rare genera may be modulated by different mechanisms. Finally, a finer timescale might make it possible to demonstrate more complicated patterns, such as periodicity (Raup and Sepkoski, 1984). However, the current number of data points should have been enough to demonstrate any biologically important patterns of this kind, and indeed it is sufficient to demonstrate the relationships leading to a dynamic equilibrium.

There are also dangers in misinterpreting the fact that diversity is regulated. On the one hand, the relevant correlations weaken considerably if the diversity data are not detrended. Thus, not only is the equilibrium dynamic, but the underlying equilibrium point evolves through time. On the other hand, the fact that a recovery in sheer taxonomic diversity will occur does not give cause for optimism about the current crisis. Any recovery will be unimaginably long on a human timescale and substantially protracted on a geological timescale. It also is clear that major mass extinctions in the past have led to enormous changes in taxonomic composition, trophic diversity, and body mass distributions that have effects for not merely tens of millions but hundreds of millions of years (Sepkoski, 1981, 1996; Jablonski, 1986a; Alroy, 2000; Todd *et al.*, 2002; Payne, 2005). Finally, the numerous anthropogenic causes of today's mass extinction are deeply unrelated to the known causes of earlier ones, so we may never be able to predict much more about the next geological era beyond the general pace of recovery in numerical terms.

MATERIALS AND METHODS

The data consist of genus counts for 48 intervals, averaging 11.0 Myr and ranging from the traditional Early Cambrian through the Neogene. These temporal bins sometimes correspond to marine stages, but often comprise sets of neighboring stages lumped to minimize variance in duration. The counts are derived from 281,491 occurrences of 18,541 genera within 42,627 fossil collections that have been sampling standardized by randomly drawing entire collections up to a quota of 15,800 specimens per bin. When the specimen count for an individual collection is not directly available, it is estimated from the occurrence count by examining rarefaction patterns for other collections in the same bin. Each collection's sampling probability is inversely weighted by its specimen count to avoid having a few large collections from a narrow range of environments and geographic areas dominate the analysis. Collections from entirely unlithified sediments are excluded. Details concerning the data and methods are reported in Alroy *et al.* (2008).

A large number of equations have been proposed to quantify origination and extinction, using paleontological data (Foote, 1994b, 2005). Traditional measures consisted of simple first and last appearance counts that sometimes were divided by some form of a diversity count to create a proportion. Proportions are biologically meaningful if they describe a sudden turnover event, but a more realistic general approach is to view turnover as an exponential decay process (Raup, 1985) and, therefore, compute instantaneous rates that are equivalent to decay constants (Alroy, 2000, in press; Foote, 2000a,b).

The problem with all existing equations is that they were developed to handle traditional compilations that only record first and last appearances. Simple range data are subject to edge effects, such as the Signor–Lipps effect and Pull of the Recent, that create systematic smearing of rates backward before a large extinction begins, smearing of rates forward after a burst of origination, and drops in extinction rates before a large sampling spike such as the Recent (Foote, 2000a). For example, backward smearing is clearly visible in family-level data on both marine and continental organisms (Benton, 1995), and the Pull of the Recent seems to amplify the downward trend in Sepkoski's genus-level extinction rates (Foote, 2000a; Peters, 2006).

Two new continuous rate equations (Alroy, in press) remove the edge effects by ignoring ranges and focusing instead on occurrence data that show which fossil taxa are actually sampled in which time intervals. These methods are only made possible by the existence of occurrence-based relational databases, and could not have been applied to the Phanerozoic marine record before the development of the Paleobiology Database (Alroy *et al.*, 2001). The new rates depend on five fundamental counts: taxa sampled at all in a focal bin (N_s), taxa sampled in a bin but not immediately before or after (one-timers, or ${}^{1}t$), taxa sampled immediately before and within the ith bin (two-timers, or ${}^{2}t_i$) or within and immediately after the ith bin (${}^{2}t_{i+1}$), taxa sampled in three consecutive bins (three-timers, or ${}^{3}t$), and taxa sampled before and after but not within a bin (part-timers, or ${}^{P}t$). The overall sampling probability P_s is just ${}^{3}t/({}^{3}t + {}^{P}t)$, where ${}^{3}t$ and ${}^{P}t$ are summed across the entire dataset.

The measures primarily used in this chapter are called three-timer rates (Alroy, in press). The three-timer extinction rate μ is $\log({}^{2}t_i/{}^{3}t) + \log(P_s)$, which expresses the exponential decay rate of a cohort crossing the base of a bin and continuing to its top, corrected for the fact that members of this cohort may be present but not sampled in the following (third) bin. The corresponding origination rate λ is $\log({}^{2}t_{i+1}/{}^{3}t) + \log(P_s)$. The same counts can be rearranged to compute a three-timer-based estimate of the extinction proportion, $1 - {}^{3}t/(P_s\,{}^{2}t_i)$. Turnover rates for the first and last intervals in the time series cannot be computed because of the structure of these equations.

These expressions assume that sampling standardization has succeeded, so P_s is uniform across all intervals, and that P_s is not systematically correlated with μ or λ. It might be if high turnover makes it harder to sample taxa in a cohort that actually originated in the immediately preceding bin (for μ) or succeeding bin (for λ). However, it can be shown by simulation that this problem is not substantial over a reasonable range of turnover rates.

Nonetheless, P_s is never completely uniform. Therefore, it is better to use separately computed values for the relevant bins. To obtain μ one uses the sampling probability for the third bin ($P_{s,i+1}$), and to obtain λ one uses the probability for the first bin ($P_{s,I-1}$). The corrected formulas $\log({}^{2}t_i/{}^{3}t) + \log(P_{s,i+1})$ and $\log({}^{2}t_{i+1}/{}^{3}t) + \log(P_{s,i-1})$ are used throughout the main analyses. This correction decreases the volatility of the turnover rates. Volatility can be quantified by averaging changes in rates between bins, i.e., for extinction taking the mean of $\mathrm{abs}(\log[\mu_{i+1}/\mu_i])$. The volatility of extinction drops from 0.778 to 0.707 with the correction, and that of origination drops from 0.824 to 0.511. Likewise, N_s is systematically related to $P_{s,i}$, and the similar correction $p_s N_s/P_{s,i}$ decreases the volatility of the diversity curve from 0.207 to 0.179.

ACKNOWLEDGMENTS

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12

Megafauna Biomass Tradeoff as a Driver of Quaternary and Future Extinctions

ANTHONY D. BARNOSKY

Earth's most recent major extinction episode, the Quaternary Megafauna Extinction, claimed two-thirds of mammal genera and one-half of species that weighed >44 kg between ≈50,000 and 3,000 years ago. Estimates of megafauna biomass (including humans as a megafauna species) for before, during, and after the extinction episode suggest that growth of human biomass largely matched the loss of non-human megafauna biomass until ≈12,000 years ago. Then, total megafauna biomass crashed, because many non-human megafauna species suddenly disappeared, whereas human biomass continued to rise. After the crash, the global ecosystem gradually recovered into a new state where megafauna biomass was concentrated around one species, humans, instead of being distributed across many species. Precrash biomass levels were finally reached just before the Industrial Revolution began, then skyrocketed above the precrash baseline as humans augmented the energy available to the global ecosystem by mining fossil fuels. Implications include (***i***) an increase in human biomass (with attendant hunting and other impacts) intersected with climate change to cause the Quaternary Megafauna Extinction and an ecological threshold event, after which humans became dominant in the global ecosystem; (***ii***) with continued growth of human biomass and today's unprecedented global warming, only extraordinary and stepped-up conservation

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efforts will prevent a new round of extinctions in most body-size and taxonomic spectra; and (***iii***) a near-future biomass crash that will unfavorably impact humans and their domesticates and other species is unavoidable unless alternative energy sources are developed to replace dwindling supplies of fossil fuels.

The Quaternary Megafauna Extinction (QME) killed >178 species of the world's largest mammals, those weighing at least 44 kg (roughly the size of sheep to elephants). More than 101 genera perished. Beginning ≈50,000 years (kyr) B.P. and largely completed by 7 kyr B.P., it was Earth's latest great extinction event. The QME was the only major extinction that took place when humans were on the planet, and it also occurred at a time when human populations were rapidly expanding during a global warming episode. Thus, the QME takes on special significance in understanding the potential outcomes of a similar but scaled-up natural experiment that is underway today: the exponential growth of human populations at exactly the same time the Earth is warming at unprecedented rates.

Causes of the QME have been explored primarily through analyzing the chronology of extinction, geographic differences in extinction intensity, timing of human arrival vs. timing of climate change, and simulations that explore effects of humans hunting megafauna (Martin, 1967; Martin and Wright, 1967; Martin and Klein, 1984; MacPhee, 1999; Alroy, 2001; Roberts *et al.*, 2001; Grayson and Meltzer, 2003; Barnosky *et al.*, 2004; Trueman *et al.*, 2005; Koch and Barnosky, 2006; Wroe and Field, 2006). Results of past studies indicate that human impacts such as hunting and habitat alteration contributed to the QME in many places, and that climate change exacerbated it. Potentially added to those megafauna stressors was the explosion of a comet over central North America, which may have helped to initiate the Younger Dryas (YD) climatic event, and which may have caused widespread wildfires, although those ideas are still being tested (Firestone *et al.*, 2007).

Whatever the cause of the QME, one thing is clear: there was a dramatic change in the way energy flowed through the global ecosystem. The energy that powers ecosystems is derived from solar radiation, which is converted to biomass. Before the extinction, the energy needed to build megafauna biomass was divided among many species. After the extinction, increasing amounts and proportions of energy began to flow toward a single megafauna species, humans.

Humans are, by definition, a megafauna species, with an average body weight of ≈67 kg for modern *Homo sapiens* and 50 kg for Stone-Age people, placing us at the lower end of the body-size distribution for megafauna

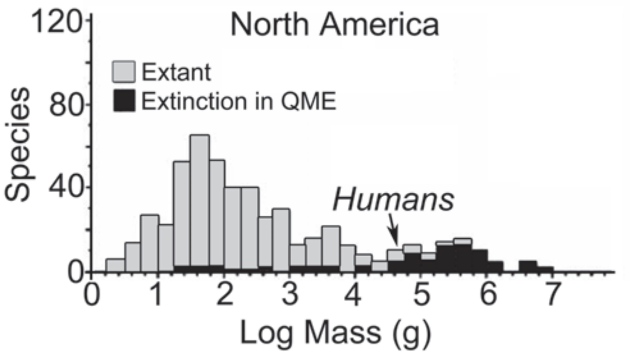

FIGURE 12.1 Body-size distribution of mammals in North America. The black bars illustrate the distribution of species that went extinct in the QME. Note that humans are at the lower end of the distribution for species that went extinct. Illustration modified from Lyons *et al.* (2004); see that source for similar distributions of fauna from other continents.

as a whole (Fig. 12.1). Previous work has demonstrated that, as human biomass grows, the amount of solar energy and net primary productivity (NPP) available for use by other species shrinks, ultimately shrinking the amount of the world's biomass accounted for by those non-human species (Vitousek *et al.*, 1986; Maurer, 1996; Vitousek *et al.*, 1997; McDaniel and Borton, 2002). Therefore, growth of human biomass should be inversely related to biomass of other species in general and to other megafauna species in particular, given that large body size itself to a large extent depends on available NPP. Such energetically driven biomass tradeoffs provide a new way to explore the QME and have the potential of extracting general principles relevant to understanding the future. That is the approach I take here, one that necessarily has many caveats (see *Methods*), but that nevertheless leads to some interesting observations.

Details of the QME and debates about its causes are summarized in recent reviews (Barnosky *et al.*, 2004; Lyons *et al.*, 2004; Koch and Barnosky, 2006; Wroe and Field, 2006). Salient points include the following. It was a time-transgressive extinction, beginning by 50 kyr B.P. in Australia and largely ending there by 32 kyr B.P., possibly concentrated in an interval between 50 and 40 kyr B.P. (Roberts *et al.*, 2001; Trueman *et al.*, 2005; Wroe and Field, 2006). In northern Eurasia and Beringia, extinctions were later and occurred in two pulses, the first between 48 and 23 kyr B.P. and the second mainly between 14 and 10 kyr B.P. (Koch and Barnosky, 2006), although some species lingered later in isolated regions (Irish elk until 7 kyr B.P. in central Siberia and mammoths until 3 kyr B.P. on Wrangel and St. Paul Island) (Guthrie, 2004; AJ Stuart *et al.*, 2004). In central North America, extinctions corresponded with the second Eurasia–Beringia pulse, starting at 15.6 kyr B.P. and concentrating between 13.5 and 11.5 kyr B.P. (Koch and Barnosky, 2006; Waters and Stafford, 2007). In South America, the extinction chronology is not well worked out, but growing evidence points to a slightly younger extinction episode, between 12 and 8 kyr B.P. (Hubbe *et al.*, 2007).

Extinction intensity varied by continent, with Australia, South America, and North America hard-hit, losing 88% (14 extinct, 2 surviving), 83% (48 globally extinct, 2 extinct on the continent, 10 surviving), and 72% (28 globally extinct, 6 extinct on the continent, 13 surviving), respectively, of their megafauna mammal genera. Eurasia lost only 35% of its genera (4 globally extinct, 5 extinct on the continent, 17 surviving). Africa was little affected, with only 21% loss (7 globally extinct, 3 extinct on the continent, 38 surviving), including at least three Holocene extinctions.

Humans evolved in Africa, and hominins have been interacting there with megafauna longer than anywhere else. Insofar as they are dated, there is no correlation between human arrival or climate change for the few African extinctions. In general, extinctions in Australia intensified within a few thousand years of human arrival ≈50 kyr B.P. but did not correspond with unusual climate change. Extinctions in northern Eurasia corresponded in time with the first arrival and population expansions of *H. sapiens*, but both pulses also were concentrated in a time of dramatic climate change, the first pulse at the cooling into the Late Glacial Maximum (LGM) and the second pulse at the rapid fluctuation of YD cooling followed by Holocene warming (Barnosky *et al.*, 2004; Koch and Barnosky, 2006). Other species of *Homo* had been interacting with the megafauna for at least 400,000 years without significant extinctions before *H. sapiens* arrived. In Alaska and the Yukon, the first pulse of extinctions corresponded with LGM cooling but in the absence of significant human presence; the second pulse coincided with humans crossing the Bering Land Bridge and with the YD and Holocene climatic events. In central North America, extinction was sudden and fast, coinciding with the first entry of Clovis hunters, the YD–Holocene climatic transition, and the purported comet explosion. In South America, humans were already present by 14.6 kyr B.P., megafauna did not start going extinct until Holocene warming commenced some 11 kyr B.P., and species of ground sloths, saber cats, glyptodonts, and horses have seemingly reliable radiocarbon dates as young as 8 kyr B.P. (Hubbe *et al.*, 2007).

Few islands ever had non-human megafauna *sensu stricto*. That, and the fact that even human biomass of islands is very small compared with the continents, caused me not to consider them in this analysis. However, it is important to note that, on nearly every island where humans have landed, extinctions (especially of birds) and wholesale habitat destruction have shortly followed.

RESULTS AND DISCUSSION

Species Loss vs. Human Population Growth

The numbers of megafauna species lost were modest until the human growth curve began its rapid exponential rise between 15.5 and 11.5 kyr B.P. (Fig. 12.2). Then, species losses accelerated, primarily in the Americas, until the non-human megafauna baseline leveled off at 183 species, where it more or less remains today. However, human population continued to rise dramatically even after the counts of non-human megafauna species stabilized.

Biomass Crash

When converted to biomass, the inverse relationship between humans and non-human megafauna is evident (Fig. 12.3). Non-human megafauna biomass fell dramatically between 15.5 and 11.5 kyr B.P., concomitant with the initial steep rise in human biomass.

Summing the biomass calculated for humans and nonmegafauna species provides a way to track changes in overall megafauna biomass through time (Fig. 12.4). The results suggest that biomass loss from the early megafauna extinctions in Australia and the first pulse of extinc-

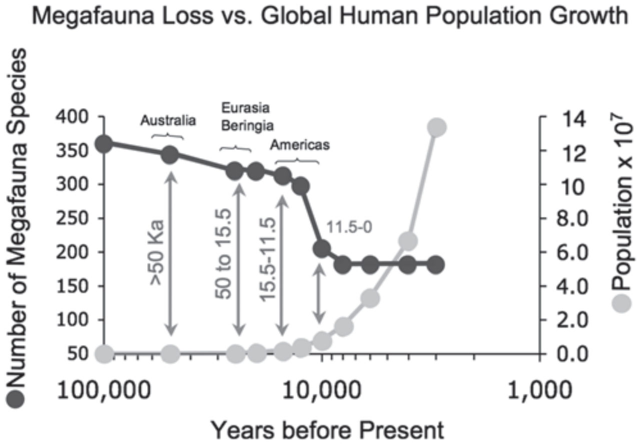

FIGURE 12.2 Number of non-human megafauna species that went extinct through time plotted against estimated population growth of humans.

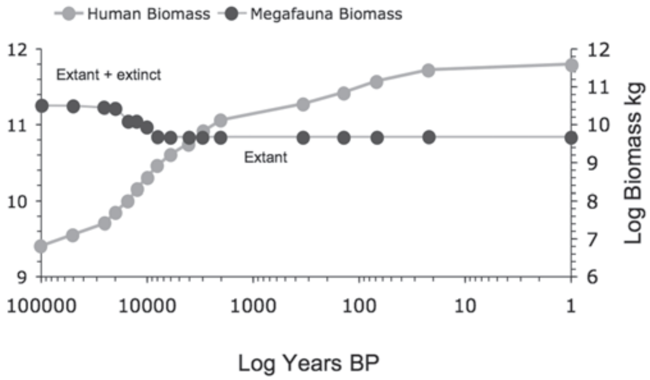

FIGURE 12.3 Estimated biomass of humans plotted against the estimated biomass of non-human megafauna. See *Methods* for parameters used.

tions in Eurasia and Beringia were almost exactly balanced by the gain in human biomass.

However, global megafauna biomass crashed dramatically between 15 and 11.5 kyr B.P. The crash reflects the second pulse of extinction in Eurasia–Beringia and the major extinction pulse in North and South America. This crash is evident in every one of the sensitivity tests, so it does not appear to be a computation artifact. The crash also remains evident when the biomass added by domestic species that support humans—pigs, sheep, goats, cattle—are included beginning 11 kyr B.P. Even using unreasonably high proportions of domesticates to humans (i.e., assuming today's

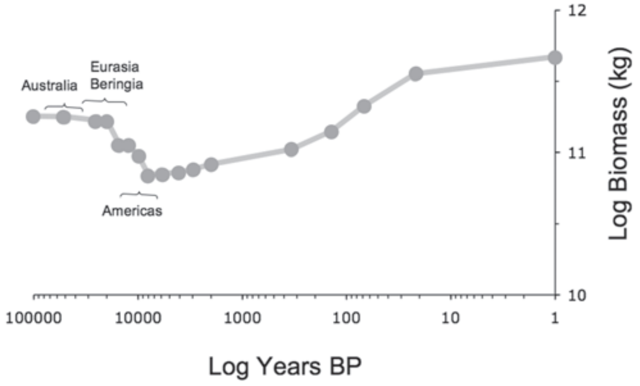

FIGURE 12.4 Change in the sum of human and non-human wild megafauna biomass through time. The brackets indicate when extinction pulses hit the respective geographic areas. See *Methods* for parameters used.

proportions even at the dawn of animal domestication) fails to make the crash disappear.

Significantly, even though human biomass was rising dramatically at the time, that rise was not enough to balance the biomass lost from the megafauna that were going extinct. Therefore, more was at work than a simple biomass tradeoff among megafauna. The suddenness of the crash, its magnitude, and its distribution across three continents suggest a global threshold event (Scheffer *et al.*, 2001; Scheffer and Carpenter, 2003). Threshold events by definition are sudden changes to alternative ecosystem states induced either by some gradual change reaching a critical value or by abnormally strong perturbations. In either case, the net effect is to push the system from one ''basin of attraction'' (in this case, a world where megafauna body mass is distributed across many species) into a different one (a world where most megafauna body mass is concentrated around humans). The cause of the QME threshold event may well reflect a synergy of reaching a critical value of human biomass at the same time that ecologically unusual perturbations came into play. The unusual perturbations included increasingly sophisticated hunting of megafauna by people, habitat alteration by growing human populations, climate changes that would have decreased total global ecological energy at least temporarily, and possibly a comet impact.

The potentially dramatic effects of hunting (so-called overkill) have been most convincingly demonstrated by simulations of the effects of Clovis hunters first entering North America (Alroy, 2001), which occurred just as global human biomass began to steeply rise. Those simulations suggest that hunting alone would result in many extinctions, because humans killed megafauna for food (Alroy, 2001).

Similarly comprehensive simulations have not yet been done for other continents, but at least indirect human impacts (including habitat alteration and fragmentation) seem likely, given the coincidence of the megafauna biomass crash after first entry or markedly increasing population sizes of humans into various regions. These coincidences include first entry of humans into South America (near 14.6 kyr B.P.) and the entry and population growth of *H. sapiens* into Eurasia (from ≈40 kyr B.P.). Entry of humans also precedes the QME in Australia, although there, both were earlier than the worldwide biomass crash. In parts of Australia (Miller *et al.*, 2005), North America (Burney *et al.*, 2005), and South America (Moreno, 2000), the evidence for indirect human impacts includes sedimentary records of increasing fire frequency, potentially indicating widespread habitat alteration through human-set fires. The indirect or direct role of humans in the QME also is suggested by the observation that the main megafauna survivors had habitat preferences that would have kept them farthest from humans (Johnson, 2002).

Also coincident with the megafauna biomass crash was rapid climatic cooling, then warming as the YD gave way to the Holocene. In the Americas, where most of the extinction was concentrated, the tail end of the LGM, then the YD cooling, depressed NPP in at least the Northern Hemisphere. A slightly earlier YD-like cooling did the same in South America, just as humans began to interact with the non-human megafauna. Likewise, YD cooling was pronounced in northern Eurasia at the time of the world biomass crash.

If the evidence for a comet explosion over North America stands the test of time, NPP available to megafauna would have been further depressed at the time of the big extinction pulse. Large tracts of land are thought to have burned, and the explosion itself may have triggered the YD cooling in the Northern Hemisphere through opening the way for massive amounts of cold glacial meltwater to flood into the North Atlantic (Firestone *et al.*, 2007).

Biomass Recovery

At the crash, megafauna biomass fell below its previous baseline value (Fig. 12.4). Then, beginning ≈10 kyr B.P., it began to build back up. By that time, the energy bottleneck that accompanied the crash was over. Global NPP was increasing as Holocene temperatures warmed, more land area was being exposed as glaciers melted, and there were fewer megafauna species on Earth among which to split the energy allocation. Even so, it took thousands of years for megafauna biomass to build back to precrash levels. The way it built back up was fundamentally different from the way it had been before, because virtually the entire recovery was by adding human biomass; the biomass of non-human megafauna remained virtually unchanged.

In terms of ecosystem dynamics under threshold models (Scheffer *et al.*, 2001; Scheffer and Carpenter, 2003), the biomass trajectory suggests that the global ecosystem crossed a threshold when the crash occurred. In the precrash state, megafauna biomass was distributed among many megafauna species, each with a relatively narrow ecological niche. In the postcrash alternative state, megafauna biomass concentrated in one species, humans, which has a very broad ecological niche. That means that ultimately humans were successful in coopting energy previously shared among other species with big bodies. It also means that not only are those extinct megafauna gone forever, but also there is no potential for new megafauna species to evolve into the "megafauna space" as long as humans are so abundant. In that respect, we have decreased biodiversity for as long as we remain abundant on Earth.

Recognizing the length of time it took the global ecosystem to recover to the precrash baseline depends on assumptions that were explored in the sensitivity tests. What I regard as the most reasonable input parameters result in the data illustrated in Fig. 12.5. That scenario includes domestic livestock, humans, and wild species as megafauna biomass and leads to two important observations.

First, the buildup of human-associated megafauna biomass, even in the absence of the extinct megafauna, took ≈9,700 years to reach precrash levels. That indicates that recovering from global ecosystem shifts takes much longer than the shift itself. Even the sensitivity test that gives the fastest recovery time (unreasonably using large carnivore density equations for all species) requires 8,000 years to reach precrash megafauna biomass. The lesson is that if another threshold causes changes as dramatic as the QME, Earth's recovery will be far in the future, and not something the next few generations would see.

Second, the point at which biomass recovery is reached is very close to the beginning of the Industrial Revolution (Fig. 12.5) or at most 700 years before that (the sensitivity test noted above). This suggests that humans were unable to exceed the normal, precrash, solar-energy-limited

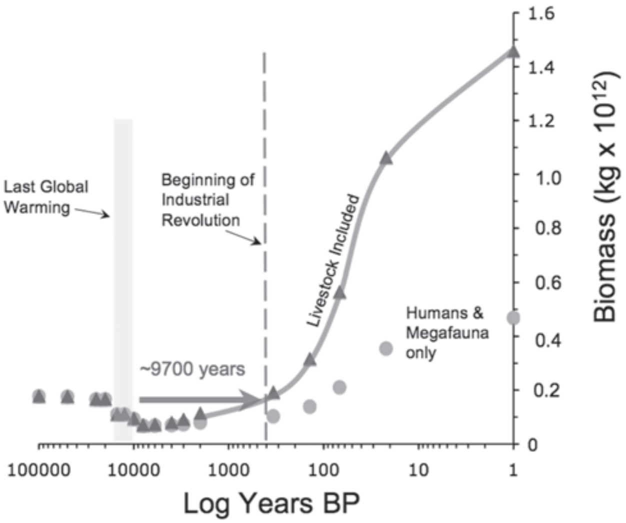

FIGURE 12.5 Semilog plot of the sum of human and non-human wild megafauna (dots) and the sum of human, wild, and domestic megafauna (triangles connected by line). Light gray bar indicates the timing of the YD-Holocene climatic event that led into the current interglacial. See *Methods* for parameters used.

baseline until we began to add to the global energy budget through mining fossil energy out of coal, oil, natural gas, and related sources. As soon as we began to augment the global energy budget, megafauna biomass skyrocketed, such that we are orders of magnitude above the normal baseline today.

CONCLUSIONS

When examined in the light of megafauna biomass tradeoffs, the cause of the QME becomes clearer, and implications for the future emerge. In essence, the QME begins to stand out not just as a major extinction event but also as an example of how threshold effects change the global ecosystem, and what new threshold events may be in sight.

In the specific case of the QME, a global crash in megafauna biomass resulted when the coincidence of at least two events constricted the share of ecological energy allotted to each non-human megafauna species. One event was a time of rapid growth in human biomass, which meant an inordinate supply of NPP began to be consumed by a single megafauna species. The other was a probable temporary reduction of NPP as the YD cooling hit both of the Americas and northern Eurasia (Hajdas *et al.*, 2003). Exacerbating the global energetic constraints were the first entry of humans into the Americas, increasingly sophisticated hunting strategies and wider disruption of habitats, and possibly a comet explosion over North America.

In the general sense, the QME has four lessons. First, the global ecosystem is in a fundamentally different state than before the megafauna biomass crash. In contrast to the distribution of resources among the 350-plus megafauna species that were alive before the QME, most of the energy available to megafauna species in the post-QME world was coopted by humans. What is left after that is being subdivided among only 183 (plus or minus) other non-human megafauna species. It is perhaps comforting from a biodiversity standpoint that those other 183 species have remained on Earth since the crash. That may speak to a reasonable amount of stability in the alternative state the global ecosystem reached after the QME threshold event, at least in pre-Industrial times. It is also consistent with the expectations of ecological threshold theory.

Second, the Industrial Revolution elevated Earth's carrying capacity for megafauna biomass. However, despite that increase in carrying capacity, ≈50% (>90 species) of those megafauna species that persisted so well for the previous 10,000 years have become extinct, critically endangered, endangered, or vulnerable to extinction in the past few decades, including >40% of the megafauna species of mammals in Africa, the only continent that made it through the QME largely unscathed. For mammals as a whole, 25% of the 4,629 species known on Earth fall in the critically endangered through vulnerable categories. This suggests that not only has all of the "extra" carrying capacity been used by humans, but also we are beginning, as happened during the QME crash, to steal from the part of the global energy budget allotted to other megafauna species. We are also going farther and using energy previously allotted to species in even smaller body-size classes. Under business-as-usual scenarios, the inevitable result will be another biomass crash that moves down the body-size classes relative to the QME event.

Third, that the normal biomass baseline was exceeded only after the Industrial Revolution indicates the current abnormally high level of megafauna biomass is sustained solely by fossil fuels. If biodiversity is actually a tradeoff between human biomass and other species' biomass, as both the QME and theoretical considerations indicate (Vitousek *et al.*, 1986, 1997; Maurer, 1996; McDaniel and Borton, 2002), then depletion of fossil fuels without replacement by alternative energy sources would mean that a biomass crash is imminent, this one depleting human biomass and causing extinction in a wide spectrum of other species. Reliable projections on the number of years into the future that fossil fuels can sustain the global ecosystem at current levels vary, but generally are in the area of 50 more years for oil, 200 more years for natural gas, and 2,000 more years for coal (Galoppini, 2006). Thus, without technological breakthroughs, the next biomass crash could be in as little as a few human generations.

Fourth, it may be no coincidence that the QME did not occur until the intersection of growing human biomass and climate change that ultimately manifested as global warming. Climate change, either cooling or warming, itself produces adjustments in geographic range distribution and population size that can lead to extinction (Barnosky, 1986; Parmesan and Yohe, 2003; Root *et al.*, 2003; Thomas *et al.*, 2004; Parmesan, 2006; Pounds *et al.*, 2006). Add to that the overall reduction of NPP that must have occurred with YD cooling, the indirect co-opting of energy by rapidly growing human biomass, and direct human displacement of megafauna by killing and habitat alteration, and the combination becomes particularly lethal. Today, we stand at a similar crossroads, because growth of human biomass in the past few decades has moved us to the point where we are beginning to co-opt resources from, further displace, and cause extinctions of species with whom we have been coexisting for 10,000 years. At the same time, Earth's climate is warming even faster than the rates of climate change that characterized the QME.

Recognizing the tradeoff between human biomass, non-human megafauna biomass, and non-human biomass in general highlights the need for extraordinary efforts to conserve the world's remaining biodiversity (McDaniel and Borton, 2002). Business as usual will not stave off severe biodiversity losses. The energetic constraints that underlie the biomass tradeoff mean that, as human biomass grows, the only way other species can persist is through conscious stepped-up efforts to save them, by such actions as setting aside reserves, enforced protection of existing reserves, and efficient and sustainable food-production practices. It is particularly urgent to act upon the knowledge that the high level of megafauna biomass today, which means humans, can be sustained only by developing alternative energy resources to replace the dwindling supply of fossil fuels.

METHODS

Dating Conventions

Unless otherwise noted, dates are expressed as calendar years before present (kyr B.P.).

Timing of Extinctions on Each Continent

I used supporting information table 1 in Koch and Barnosky (2006) to place the extinction of each megafauna species in one of the following temporal bins: <100 kyr B.P., 100–50 kyr B.P., 50–15.5 kyr B.P., 15.5–11.5 kyr B.P., and 11.5–0.5 kyr B.P. The latter bin is cut off at 500 years ago to exclude recent extinctions. As far as is known, before 500 years ago, the last megafauna species extinction was 3,000 years ago. Despite being somewhat coarse, these bins are adequate to examine the biomass tradeoff at the order-of-magnitude level of resolution to which the rest of the data are appropriate.

Estimating Human Biomass

Hern (1999) provided estimates of the numbers of hominins on Earth from the approximate first appearance of *Homo habilis* some 3 million years ago up to the number of *H. sapiens* projected to occur in approximately the year 2455. His estimates, based on calculating doubling times for hominin and human populations, were constrained by the fossil record of human evolution, by archaeological information, and by historical and demographic records up to 1999. I used his estimates for the numbers of people on Earth at a given point in time and multiplied that by the average weight of a person to estimate global human biomass for each time slice of interest. Following logic detailed in Hern (1999), average weight for a human was considered 50 kg up to ≈400 years ago, and 67 kg thereafter.

Estimating Non-Human Megafauna Biomass

In principle, megafauna biomass for a given species is calculated by multiplying the average body mass by the number of individual animals. To estimate this and produce the figures in this chapter, I used the following parameters. Average body mass values were taken from a recent compilation (Smith *et al.*, 2003). For the few species not listed in that compilation, I used values for similarly sized animals that were listed. Number of individual animals per species was estimated in the following way. First, there is a correlation between body mass and population density, that is, individuals per km^2 (Damuth, 1993; Silva and Downing, 1995; White *et al.*, 2007). To estimate density, I used regressions from Silva and Downing (1995): for large herbivores, density = $-0.44 \times \log$(kg body mass) + 1.01; and for large carnivores, density = $-1.31 \times \log$(kg body mass) + 1.22. Second, megafauna species typically have geographic range sizes that average between 7% and 9% of the area of the continent on which they live. For Australia, I estimated the geographic range size of each megafauna species to be 7.8% of the continental area, or ≈600,000 km^2 (Murray and Dickman, 2000). For Africa, Eurasia, North America, and South America, geographic ranges sizes were set to 8.6%, 8.1%, 8.2%, and 7.2% of the respective continental areas (Letcher and Harvey, 1994; Smith *et al.*, 1994; Brown, 1995). For each species, estimated density was multiplied by estimated geographic area to give an approximate number of individuals, which was then multiplied by estimated mass per individual.

Continental area was not constant through the time spanned by the QME, because during glacial times, nearly one-half of North America, about one-tenth of Europe and northern Asia, and a small percentage of South America were covered by glaciers. This loss of land was offset only to a very small extent by the exposure of currently submerged land with the lower sea level of glacial times. To account for varying continental area in the estimates of geographic range size, continental area during glacial times was considered to be 50% of its current size for North America, 90% of its current size for Europe and northern Asia, and 95% for South America. For the transitional time ≈10 kyr B.P., area for these continents was set at the intermediate values of 75%, 0.95%, and 98% of their current respective sizes.

Biomass of Domestic Stock

To obtain a maximum value for the biomass of domesticated megafauna, I calculated the present proportion of human biomass to domestic stock biomass as tabulated by Hern (1999). I then used that proportion to back-calculate the maximum biomass of domestic stock, given the estimated biomass of humans, going back to 10.5 kyr B.P., by which time pigs, goats, sheep, and cattle were first domesticated (Pedrosa *et al.*, 2005; Beja-Pereira *et al.*, 2006; Chen *et al.*, 2006; Fernandez *et al.*, 2006; Larson *et al.*, 2007). For time slices up to 6 kyr B.P., only pigs, goats, and cattle were included in the domestic livestock count. More recent time slices also included horses, buffalo, camels, chickens, ducks, turkeys, and catfish. Clearly for prehistoric times, this method provides an overestimate of domestic stock biomass, because no one would argue that the first ranchers had as many domestic stock per person as is the case presently. However, because the purpose of this part of the analysis was to see whether domestic stock compensated for a reduction in wild megafauna, the overestimation actually makes the conclusions more robust.

Sensitivity Tests

Sensitivity tests were conducted to assess how robust the general trends were to varying assumptions about density and geographic range size, on which the calculated biomass value for each species depends. Calculated density was varied by applying the regression equation for large carnivores (Silva and Downing, 1995) to the whole dataset at one extreme (results in least biomass), by applying the regression equation for large herbivores (Silva and Downing, 1995) to the whole dataset at the other extreme (results in most biomass), and by applying an average density equation to all species, density = –0.77 × log(g body mass) + 3.98 (Damuth, 1993). One test also assumed a 10% increase in density of the megafauna that survived after the QME. Assumed geographic range size for each species was variably set between ≈9% and 5% of the area of the continent on which the species lived. Varying these parameters does not alter the general trend of biomass change through the QME. Varying them does affect the absolute values calculated for biomass and the amount of time indicated for biomass recovery but not in ways that obviate the main conclusions of this chapter.

Caveats

Methods used here are intended to give simply an order-of-magnitude indication of how biomass changed through time and identify times of major biomass crash and recovery. The calculations are necessarily coarse. Exact values change given different inputs to the estimations, but the sensitivity tests make it seem unlikely that the important trends are simply estimation artifacts. Additional refinements would be desirable but are beyond the scope of this initial work. Such refinements ideally would include body mass vs. density regressions tailored to each species, refining the geographic range estimates for each species through niche modeling, and assessing details of the relationship among megafauna biomass, potentially available NPP, and available solar energy as estimated from climate and vegetation models. It would also be useful to accumulate region-by-region estimates of both human and non-human biomass through time. Despite leaving room for such refinements, this first effort highlights some overall trends that appear robust.

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Part IV

PROSPECTS FOR THE FUTURE

Armed with evidence from the past and present about global patterns and processes of extinction, what can be projected for global biodiversity in the near and distant future? Chapters in this section address several of the many challenges presented by the ongoing extinction crisis, both for the biodiversity sciences *per se* and for efforts to translate the science into an enhanced societal awareness that might spawn effective conservation policies and actions.

Conventional wisdom has been that ecologically important traits (such as an ability to withstand cold climates) are too evolutionarily labile to be of much utility in phylogenetic inference. In Chapter 13, Michael Donoghue challenges this paradigm by reviewing several cases in which higher plant taxa have retained, for long periods of evolutionary time, particular traits that impact their geographic distributions. Donoghue calls this phenomenon "phylogenetic niche conservatism." His basic idea is that the geography of biodiversity at any horizon in time reflects an *interaction* between phylogenetic legacy (as registered in the evolved ecological characteristics of particular lineages) and contemporary ecological selection pressures. This worldview implies that evolutionary shifts from one ecological setting to another cannot be readily accomplished by many plant taxa, especially if substantial genetic adjustments in physiology are required. Thus, newly opened niches are more likely to be filled by immigrants from ecologically similar zones than by *in situ* evolution of local populations. Donoghue addresses some ramifications of phylogenetic niche conservatism for the future of plant biodiversity in the face of global climate change and habitat fragmentation.

In a somewhat similar vein, Jonathan Davies and colleagues associated with the Andy Purvis group show in Chapter 14 how a phylogenetic modeling approach can help to identify mammalian taxa whose intrinsic biology might lend them especially vulnerable to environmental pressures. They begin by combining phylogenetic information from a recently completed Tree of Life for mammals with ecological, life history, and geographic data to examine the origins and current distributions of mammalian biodiversity. Results from the analysis indicate that evolutionary cradles of origin have shifted over time, and that extinction risks vary according to the type of mammal (e.g., large-bodied versus small-bodied) and also to spatial and temporal differences (often region-specific) in threat intensity. The authors discuss ramifications of such phylogenetic findings for the near- and long-term future of mammalian biodiversity, including how alternative criteria (different "currencies of conservation") might be used in setting preservation priorities.

Before the mid-20th century, scientific analyses of biodiversity rested on appraisals of organismal phenotypes. That situation changed dramatically when molecular techniques were introduced that permitted direct assays of genotypes. The molecular revolution in evolutionary biology has provided powerful tools for biodiversity assessments ranging from species identifications and phylogeny reconstructions to genetic dissections of ontogeny. Projecting forward, in Chapter 15 John Avise describes three opportunities for the field of biodiversity genetics that seem not to have been widely appreciated or discussed: use information from the emerging phylogenetic Tree of Life to erect the first-ever universally standardized scheme of biological classification; identify biogeographic hotspots and centers of origin (including those tracing to the late Tertiary) for various extant biotas; and engage in educational outreach by conveying to students and the public a sense of wonder and appreciation for the marvelous workings of nature, many of which are being revealed for the first time by genetic appraisals. Capitalizing on these opportunities should be instructive for basic science and also helpful in conservation efforts.

In Chapter 16, Michael Novacek expands on the public-outreach mission for conservation biology by emphasizing the need to awaken a broad audience to the ongoing biodiversity crisis. Despite the urgency of current environmental problems, and committed efforts (albeit by relatively small segments of society) over the past 20 years to find solutions, national and international responses to date have been slow to materialize and inadequate to steward global biodiversity through the crucial 21st century. One major reason is the general lack of understanding and engagement on biodiversity issues by the public, which in polls typically ranks environmental concerns below other challenges such as terrorism, the economy, and family values. Novacek analyzes this state of affairs and argues that effective ways must be found to tailor biodiversity messages to each target audience. Enlightened environmental measures by corporations and democratic governments will be achieved only if the "power of the people" is marshaled in favor of conservation efforts.

In Chapter 17, Peter Bryant canvasses the many ways that the general public can become engaged in conservation efforts. Using Orange County—the second most populous county in California—as a touchstone, he explains how local citizens have played and are continuing to play important roles in identifying species of plants and animals, monitoring the status of local populations, assessing geographic distributions, monitoring migration patterns, contributing to rescue and restoration efforts, educating students, joining conservation organizations, promoting parklands and other preservation initiatives, and otherwise contributing to the assessment and protection of biodiversity. These examples are heartening because Orange County (with three million people and growing) lies in one of the most heavily urbanized regions of North America, yet still retains substantial biodiversity that at least some segments of the public are beginning to appreciate and strive to protect.

In Chapter 18, Paul Ehrlich and Robert Pringle close this book by reminding us that "the fate of biological diversity for the next 10 million years will be determined during the next 50–100 years by the activities of a single species" (*Homo sapiens*). With the projected increase by mid-century of 2.6 billion people to an already overcrowded planet, the prospects for preserving substantial biodiversity are dim, unless societal mindsets and comportments change dramatically and quickly. The authors issue a pluralistic call for action on seven fronts: combat the underlying drivers of biodiversity loss (notably human population growth, overconsumption, and the use of malign technologies); promote permanent nature reserves; provide social and economic incentives to preserve wild populations; better align economies with conservation; restore biodiversity on currently degraded lands; vest human occupants of a region with the desire and capacity to protect nature; and, in general, fundamentally transform human attitudes toward nature and biodiversity. These calls are ambitious, but positive societal responses to them are not yet beyond the realm of possibility.

13

A Phylogenetic Perspective on the Distribution of Plant Diversity

MICHAEL J. DONOGHUE

Phylogenetic studies are revealing that major ecological niches are more conserved through evolutionary history than expected, implying that adaptations to major climate changes have not readily been accomplished in all lineages. Phylogenetic niche conservatism has important consequences for the assembly of both local communities and the regional species pools from which these are drawn. If corridors for movement are available, newly emerging environments will tend to be filled by species that filter in from areas in which the relevant adaptations have already evolved, as opposed to being filled by *in situ* evolution of these adaptations. Examples include intercontinental disjunctions of tropical plants, the spread of plant lineages around the Northern Hemisphere after the evolution of cold tolerance, and the radiation of northern alpine plants into the Andes. These observations highlight the role of phylogenetic knowledge and historical biogeography in explanations of global biodiversity patterns. They also have implications for the future of biodiversity.

The rise of phylogenetic biology has revolutionized the study of molecular and developmental evolution, but has still had rather limited impact in ecology. Interest in phylogeny is growing within community ecology, but it has received almost no attention among eco-

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system ecologists [however, see Edwards *et al.* (2007)]. It is possible that knowledge of phylogeny is less relevant in these areas, but it seems more likely that the most productive intersections have not yet crystallized. Recent work on community phylogenetics, and emerging ideas on the integration of historical biogeography in studies of biodiversity, may be yielding a key principle governing the historical assembly of communities, which could in turn provide the basis for a new synthesis of phylogeny and ecology. Put simply, it may often be easier for lineages to move than it is for them to evolve. My essay is an attempt to better characterize this principle and explore some of its consequences for global diversity patterns and the future of biodiversity.

REFLECTIONS ON THE EVOLUTION OF ECOLOGICAL TRAITS

When I began studying phylogenetic systematics in the late 1970s, it was widely believed that ecologically important traits were too labile to be of much use in phylogenetic inference. The feeling was that such characters were so prone to homoplasy that they would be positively misleading about relationships; instead, one should concentrate on characters that lack obvious functional value [Mayr (1969) called this the "Darwin principle"]. The rapid rise of the use of molecular data was partly a function of the belief that molecular characters were less subject to selection and would therefore better reflect evolutionary history. Arguments were made against this view on the grounds that it was hard to judge the phylogenetic value of characters at the outset of an analysis [e.g., see Hennig (1966)]. However, in general, such arguments had rather little impact on the overall mindset; homoplasy was viewed as bad for phylogenetics and "ecological traits" were viewed as especially prone to homoplasy.

Where did this view come from? Within systematic biology one line of reasoning was that groups that were placed at higher taxonomic ranks (e.g., families, orders) showed little uniformity with respect to the environments that they occupied. This was said to be especially true in plants. For example, Arthur Cronquist, the prime architect of angiosperm classification in that era (from the 1960s through the 1980s), pointed out repeatedly that higher taxa were not readily characterized by particular ecological roles: "Each of the obvious ecological niches for land plants is occupied by species representing diverse families and orders. . . . Conversely, a single family may fill widely varying ecological niches" (Cronquist, 1968). Instead, higher taxa tended to be more uniform in minute details of their flowers and fruits, which remained constant through transitions into disparate environments. Cronquist referred especially to the Asteraceae (sunflower family) for support, noting that its members are marked by totally obvious reproductive characters, but vary from being trees, to shrubs, vines, succulents, and perennial and annual herbs, which grow from tidal to alpine zones, from the equator nearly to the poles. He concluded from such cases that "the obvious adaptive changes that can take place mostly occur so easily and frequently that they tend to mark species and genera rather than larger groups" (Cronquist, 1968).

Ledyard Stebbins, whose 1974 book on the macroevolution of flowering plants dominated discussions for decades, held much the same view. That is, he argued that owing ultimately to limited functional and developmental integration in plants, vegetative traits related to climate tolerances were highly labile and only rarely marked higher taxa. In fact, his main thesis depended directly on the rapidity with which transitions between major climate zones could occur. He argued that major evolutionary changes occurred in ecotones or climatically marginal zones, and that tropical rain forests were therefore "museums," not "cradles." As he appreciated, this required "extreme ecological plasticity" and genetic adaptation to moister or drier climates with "relative ease" (Stebbins, 1974).

Growing up with these views, and having passively accepted them, I remember being surprised by several later findings. Whereas I fully expected reproductive traits to show less homoplasy than vegetative traits that seemed to be linked more directly to climate variables (e.g., leaf margins, pubescence), a meta-analysis of homoplasy in published plant phylogenies failed to demonstrate such a difference (Donoghue and Sanderson, 1994). In fact, levels of homoplasy in phylogenetic studies rarely seem to correspond to standard intuitions about lability or selective value. Instead, homoplasy seems to be positively correlated primarily with the number of terminal taxa included in analyses [e.g., Sanderson and Donoghue (1989)] and limitations on the number of character states (Donoghue and Ree, 2000).

Even more surprising was the finding by Campbell Webb (2000) that the trees occupying 0.16-hectare plots in a rainforest in Borneo seemed to be more closely related to one another than expected by chance assembly from the regional species pool of 324 tree species. Given that these plots differed with respect to key environmental variables (some were located in swampy areas, some on ridge tops, etc.), one interpretation is that there are subtle, previously underappreciated, ecological similarities among related plants, both above and below the traditional rank of family. In retrospect, this can be reconciled with Cronquist's observations simply by allowing that shared ecological niche characteristics exist, but that the phylogenetic distribution of these does not correspond well with particular named clades or taxa assigned to a given taxonomic rank.

In general, comparisons centered on taxonomic ranks have hidden the connections between phylogeny and ecology. In fact, some traditional taxonomic families are generally associated with particular environments; for example, Poaceae (the grasses) in grasslands, Ericaceae (the heaths) in heathlands, and Zosteraceae (the sea grasses) in the sea. The plant clade I know the best, the Dipsacales, ancestrally occupied northern temperate forests, but Dipsacaceae have specialized in drier habitats, especially around the Mediterranean basin, and Valerianaceae have adapted to alpine habitats (Donoghue *et al.*, 2003). But there are also ecologically distinctive clades within traditional families: multiple mangrove lineages, dry-adapted Euphorbiaceae, and bamboos and multiple C4 lineages within grasses, to name just a few examples. Likewise, there are ecologically distinguishable clades comprised of a number of related families. Core Caryophyllales provide an example, mostly being adapted to arid or high-salinity habitats (e.g., the "portulacaceous alliance" of families, which includes the Cactaceae). The several insectivorous families within Carophyllales *sensu lato* present another clear case, as do those of the "aquatic clade" within Alismatales, and the parasitic plants of Santalales.

Moreover, it is important to appreciate that the findings of Webb (2000) and others (see below) do not depend on all members of a clade occupying the same habitat, but rather on a tendency for members of a clade to be more similar with respect to the environments that they occupy. From this perspective the link between phylogeny and ecology becomes even clearer. After all, major clades within angiosperms, despite significant ecological diversity, hardly occupy all possible environments, but instead are restricted to one or a few major biomes, such as tropical rainforests, temperate forests, grassland, or deserts. Despite the great variety of environments occupied by the Asteraceae, for example, they are far more common in arid environments than they are in tropical forests. Such tendencies are well known to field botanists, but have only recently been subjected to analysis. In the most comprehensive study to date, Prinzing *et al.* (2001) demonstrated far higher than expected levels of niche conservatism in the plants of Central Europe.

Such ecological correlations (especially those at the level of major clades) imply that evolutionary shifts from one ecological setting into another, where these require substantial physiological adjustments, are not so readily accomplished as one might have imagined, homoplasy in ecological traits notwithstanding. Consider one example: the evolution of cold tolerance. Many plant lineages have managed to adapt to cold, highly seasonal climates, but it is also true that only a subset of ancestrally tropical plant lineages have succeeded in making this transition (Judd *et al.*, 1994). That is, many tropical plant groups are strictly tropical [e.g., half of the families of flowering plants have no temperate representatives; Ricklefs and Renner (1994)] and have not spread out of the tropics despite presumably having had ample opportunity to do so with the expansion of temperate climates (or the contraction of the tropics) during the Tertiary (Fine and Ree, 2006). The implication is that it is not so easy to evolve tolerance to freezing temperatures and highly seasonal environments. In fact, such adaptations do appear to require a coordinated set of physiological adjustments, including (in most cases) biochemical changes to maintain a fluid lipid layer for the rapid transfer of water out of cells to avoid ice crystals forming in the cytoplasm, and the deployment of special proteins and sugars to stabilize membranes when cells become desiccated and condensed (Sakai and Larcher, 1987; Körner, 2003).

Overall, my impression of ecological traits is that they show the same wide range in evolutionary lability as do morphological traits. On one end of the spectrum there are extremely labile traits of the sort that ecologists and population geneticists have tended to concentrate on. On the other end there are ecological traits of the sort I have highlighted above, which are evolutionarily much more conserved, perhaps because their evolution entails the modification of complex, highly integrated physiological systems. Recent phylogenetic studies have simply focused new light on the existence and the global importance of key ecological traits at the more conservative end of this distribution. My concentration here on the conserved end of the distribution is in no way meant to question the reality or significance of highly labile ecological traits, the evolution of which surely underlie many ecological adjustments.

PHYLOGENETIC NICHE CONSERVATISM (PNC)

What Harvey and Pagel (1991) termed PNC refers to the expectation that, all else being equal, related species will tend to occupy the same sorts of environments (Wiens and Graham, 2005). PNC is not meant to imply that ecological barriers are insurmountable, or even that niche shifts are rare. Niche evolution obviously occurs, and may even be the norm under certain circumstances [e.g., Losos *et al.* (2003)]. However, PNC, to the extent that it exists, does imply that speciation can occur regularly without major niche shifts [e.g., Peterson *et al.* (1999)]. Furthermore, under the assumption that opportunities to undergo major shifts have regularly presented themselves, PNC implies that these opportunities have not been seized so readily that high-level eco-phylogenetic correlations are completely overridden by ongoing low-level niche shifting. Although, strictly speaking, it is not necessary to link PNC with the view that there are constraints on niche evolution, I believe that it is the relative difficulty of making major ecological shifts that explains the patterns I have highlighted above, and which, as discussed below, render PNC especially consequential in explaining the distribution of biodiversity.

An example of the potentially significant role that PNC plays in structuring the distribution of biodiversity relates to discussions of the latitudinal species diversity gradient [reviewed by Mittelbach *et al.* (2007)]. One longstanding hypothesis has been that this pattern is underlain by a simple historical cause, namely a longer time for diversification in the tropics in many lineages than outside of the tropics. If many extant lineages originated and began their diversification under tropical climatic conditions, and if movements of these lineages out into temperate climates occurred only more recently, this alone would go a long way toward explaining the gradient [e.g., Farrell *et al.* (1992), Latham and Ricklefs (1993), Wiens and Donoghue (2004), Jablonski *et al.* (2006)]. Rangel *et al.* (2007) put this verbal argument to the test in a simulation focused on bird biodiversity in South America, showing that realistic patterns can be obtained under a variety of circumstances.

A key ingredient of this argument, which led John Wiens and I to call it the "tropical niche conservatism" hypothesis (Wiens and Donoghue, 2004), is that not all tropical lineages confronted with the retraction of tropical climates during the Tertiary managed to adapt to colder climates. Instead, many of these lineages simply tracked tropical habitats, and therefore became increasingly geographically restricted. If every tropical lineage had been able to readily adjust to cold temperatures and extreme seasonality, then the latitudinal diversity gradient would be far less steep than the one we observe today. This is the important sense in which PNC has explanatory power beyond the time-for-speciation factor.

NICHE CONSERVATISM AND LOCAL COMMUNITY ASSEMBLY

That there should exist a general relationship between phylogenetic relatedness and ecological interactions that are crucial to community assembly, has been evident from Darwin (1859) onward. As G. Evelyn Hutchinson put it (Hutchinson, 1965): "It is evident that at any level in the structure of the biological community there is a set of complicated relations between species, which probably tend to become less important as the species become less closely allied. These relations are of the kind which ensure niche separation." With the rapid expansion of phylogenetic knowledge [e.g., see Cracraft and Donoghue (2004)], it has now become possible to study this rigorously.

A series of recent analyses imply that PNC influences community composition both by the filtering of the regional species pool based on abiotic niche parameters and through competition and other biotic interactions. The signals of these processes may be reflected in the distribution of species across the phylogeny of the regional species pool [quantified using a variety of phylogenetic diversity measures; Faith (1992a), Webb (2000), and Webb *et al.* (2007); www.phylodiversity.net/phylocom]. As Webb *et al.* (2002) and Cavender-Bares and Wilczek (2003) reasoned, where abiotic habitat filtering is the dominant force shaping coexistence, PNC should result in phylogenetic clustering in the phylogeny of the regional species pool. On the other hand, where biotic competitive exclusion is the dominant ecological force, PNC should result in a more even (overdispersed) distribution of species on the regional tree than expected by chance.

These relations may hold in the abstract, and have oriented the interpretation of a number of studies [e.g., Cavender-Bares *et al.* (2004), Ackerly *et al.* (2006), Slingsby and Verboom (2006)], but there are a variety of complications or necessary extensions. For example, as Webb *et al.* (2002) and Cavender-Bares and Wilczek (2003) appreciated, an overdispersed phylogenetic pattern can also result from abiotic filtering from an underlying phylogeny showing convergent niche evolution. This observation simply highlights the need to couple such studies with independent phylogenetic tests of the extent of PNC in the clades under consideration [cf. Cavender-Bares *et al.* (2006) and Slingsby and Verboom (2006)]. Likewise, "ecological facilitation," rather than competition, might underlie an overdispersed phylogenetic pattern (Valiente-Banuet and Verdu, 2007), again emphasizing that there is not a simply one-to-one relationships between a phylogenetic pattern and an underlying cause.

It is also clear that possible causal processes will vary in intensity, and even in kind, as a function of scale (Swenson *et al.*, 2007). For example, Webb *et al.* (2006) hypothesized that seedling phylodiversity patterns within small rainforest plots reflect the sharing of fungal pathogens among close relatives, whereas at a larger scale in the same forest they found evidence of habitat filtering. Cavender-Bares *et al.* (2004, 2006), in studies centered on oaks (*Quercus*) in northern Florida, showed evidence for phylogenetic evenness at smaller spatial and taxonomic scales (interpreted as the outcome of competition), but phylogenetic clustering at larger scales (interpreted as habitat filtering of phylogenetically conserved ecological traits). Clearly, sorting out among such possibilities requires the development of appropriate null models, and simulations to evaluate the power to distinguish alternative explanations [e.g., Kembel and Hubbell (2006) and Kraft *et al.* (2007)].

For present purposes it is especially important to note that entirely different causal factors become relevant as such studies scale up to much broader regions, or focus on clades that have moved around the globe. For example, Forest *et al.* (2007) reported lower phylogenetic diversity (despite higher species diversity) in the western Cape flora of South Africa, in part as a function of multiple rapid radiations (Linder, 2005). In contrast, the eastern Cape showed higher phylodiversity, in part because it interdigitates with another biodiversity hotspot. The key point is that at such larger scales historical factors such as speciation, extinction, and biogeographic boundaries become highly relevant.

NICHE CONSERVATISM AND REGIONAL SPECIES POOLS

A less well appreciated role of phylogenetic niche conservatism, and the one that I especially want to highlight here, concerns the composition of the regional species pools from which local communities become assembled. In my view the most compelling studies to date along these lines have been carried out in Mediterranean climate systems, by Miguel Verdu *et al.* (2003) and David Ackerly (2004), both building on the seminal work of Carlos Herrera (1992).

I will focus here on Ackerly (2004), as his study concerned a single region, the California chaparral. His analyses of a number of signature woody chaparral clades suggested that in many cases the characteristic adaptive traits were evolved well before the advent of the Mediterranean (summer dry) climate some 3 million to 5 million years ago. Plants with these characters (or their similar precursors) were either present in the vegetation of that region beforehand, or they moved in from outside the region, perhaps from dry areas further to the east and south (''mexical'' vegetation), as opposed to evolving *in situ* in response to the changing climate. That is, many characteristic elements of the flora (e.g., *Ceanothus*, *Arctostaphylos*), and consequently many of the traits that we associate with chaparral (e.g., thick, sclerophyllous leaves), resulted from the sorting of species with relevant adaptations already in place, which then adjusted to the new rainfall regime by shifts in the timing of growth and reproduction. In a few lineages (e.g., *Adenostoma*, *Heteromeles*), however, chaparral leaf features probably did evolve *in situ*. Interestingly, many of the elements that filtered into the flora have Madrean-Tethyan affinities (Axelrod, 1975) and were preadapted to hotter, arid conditions, whereas those showing *in situ* adaptation derive mainly from temperate Northern Hemisphere lineages. In other words, it appears that the composition, structure, and function of the chaparral as we know it today reflects the characteristics of prechaparral vegetation and the biogeographic source areas that were accessible as the climate materialized.

IT'S EASIER TO MOVE THAN TO EVOLVE (UNLESS IT ISN'T)

These studies suggest what may be a general principle, namely that under many circumstances it may be easier for species to migrate into an area with at least some of the relevant adaptations having already evolved, than it is for those adaptations to evolve in place. This formulation highlights two key variables, namely the rate of trait evolution in relation to the rate of dispersal. But, the existence of relevant geographic/climatic connectivities through the relevant time period is critical to the general model and to specific outcomes. If, when climate change occurs, suitable corridors exist for the dispersion of species with relevant traits, these lineages will tend to track the habitat to which they are adapted and move into the region relatively quickly, perhaps preempting the *in situ* evolution of these traits among the natives. Under these circumstances, it is the sorting or filtering of species into the region that will dominate the assembly of the regional species pool.

On the other hand, if plants with relevant adaptations do not already exist in an area undergoing environmental change, and if corridors for the movement of relevant plants are missing at the right times and places, then adaptations will presumably evolve within the resident lineages. Oceanic islands, of course, provide classic cases of such isolation and of the ecological radiations of those species that did manage to establish [e.g., Carlquist (1974) and Baldwin and Sanderson (1998)]. But, as Ackerly (2003) has argued, isolation by distance can also occur in continental settings (e.g., isolated mountaintops, peculiar edaphic circumstances), and "environmental islands" that are discontinuous in realized environmental space from surrounding habitats can similarly promote adaptive divergence.

Major physiological/morphological adaptive shifts certainly have occurred, sometimes frequently, and sometimes even rapidly, perhaps especially in relative isolation. My argument is that under circumstances of habitat continuity that promote migration, movement into an area experiencing change is often likely to occur before resident species adapt to the circumstances. It is a question, then, of the interplay of historical circumstances either favoring or disfavoring the movement of lineages from habitats outside of a region, with the relative ease or difficulty of evolving the suitable ecological characters. If movement into the area is difficult, and the relevant adaptive shifts are easy, then *in situ* evolution will predominate. My assertion is simply that corridors have often been present, and that adaptations to major new climates have often been somewhat difficult.

The existence of corridors at the right times and places not only provides a mechanism for community assembly but also helps to explain PNC itself. Under these circumstances, stabilizing selection may be a key factor in maintaining ecological tolerances. If corridors did not exist and isolation were correspondingly increased, *in situ* evolution and local extinction would probably increase and PNC would be less commonly observed. That is, there is a connection between environmental connectivity and niche conservatism, on the one hand, and between isolation and convergent ecological adaptation on the other [*cf.* Wiens *et al.* (2006)]. In this sense, historically contingent connectivities have played a more central role than we might have imagined in mediating the tradeoff of dispersal and evolutionary change, and, thereby, in generating the patterns of biodiversity that we see today.

A key question that has still received only limited attention, concerns the circumstances in addition to isolation that will favor adaptive niche evolution. Ackerly (2003), for example, highlighted the evolutionary opportunities that may present themselves along the "trailing edge" of a species that is shifting its geographic range in response to changes along a single environmental axis (e.g., temperature). This mechanism depends to some extent on a barrier preventing immediate occupancy by species that are appropriately adapted to the new conditions. Here, too, it is the balance of the ease of movement in relation to the ease of adaptation that determines the outcome.

THREE EXAMPLES

I believe that the simple idea outlined above provides the basis for a much fuller understanding of global biodiversity patterns, and that phylogeny and PNC will therefore play a much larger role in explaining such patterns. Here, I briefly highlight three biodiversity phenomena in flowering plants that variously reflect the interaction of niche conservatism with environmental changes through the Tertiary (Fig. 13.1).

The first example concerns the disjunction of clades among the major tropical regions of the world. Although many of these cases, especially involving South America and Africa, have traditionally been attributed to the breakup of Gondwana, recent studies have shown that in many (perhaps most cases) the relevant lineage-spliting events are too young. Instead, there must have been movements among these regions after the breakup was well along. An example is provided by Malpighiaceae, which is most diverse in the New World tropics but has several lineages in tropical Africa (and Madagascar) and Asia. Analyses by Davis *et al.* (2002, 2004) demonstrated that this distribution reflects several disjunctions, in widely separated clades, and that these were, on the whole, too young to have been caused by the spreading of the Atlantic. The presence of fossils in several places in the Northern Hemisphere, where Malpighiaceae no longer occur, combined with evidence on paleogeography and the greatly expanded northern limit of tropical climates and vegetation in the Eocene [e.g., Fine and Ree (2006)], favor the movement of several lineages from the New World tropics into the Old World tropics through a Laurasian corridor of tropical climates in the early Tertiary.

The modern disjunct distribution is largely, therefore, a result of the southward retreat of these plants as tropical climates receded in the Oligocene and Miocene. The key point is that, perhaps despite "trailing edge"

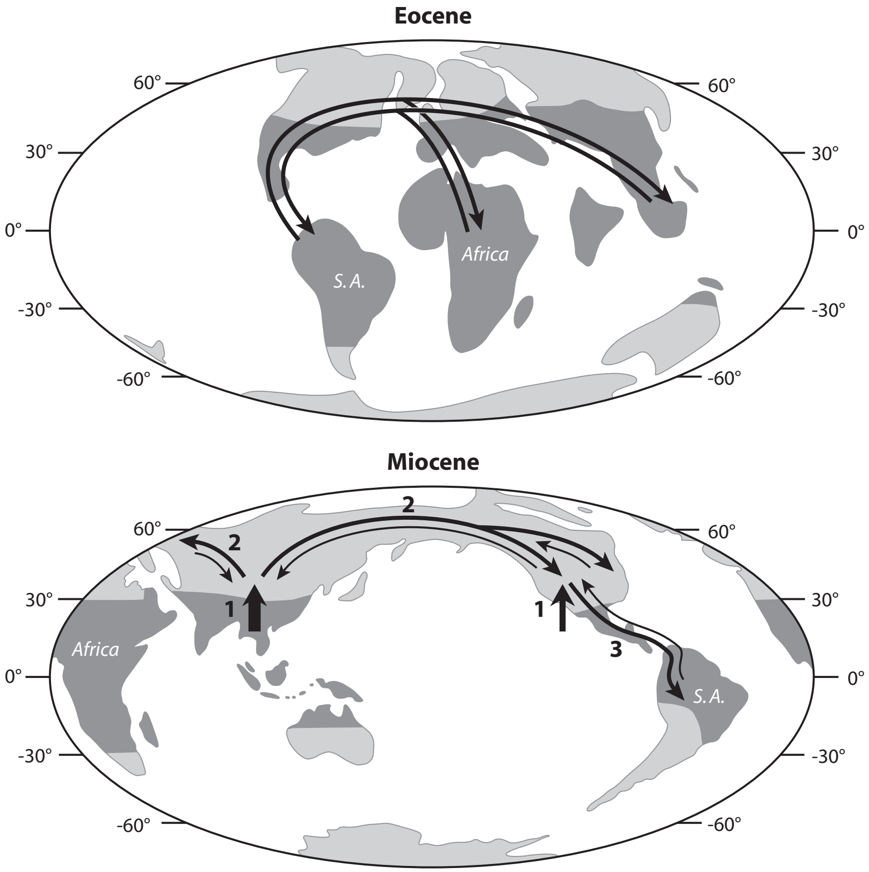

FIGURE 13.1 Major patterns in the movement of plant lineages discussed here. (*Upper*) Hypothesized movements in both directions of now disjunct tropical lineages across the North Atlantic during the early Tertiary. (*Lower*) (1) Hypothesized originations of adaptation to cold, seasonal climates, perhaps predominantly in Asia. (2) Iterated movement more recently of temperate lineages around the Northern Hemisphere, especially through Beringia, and perhaps predominantly out of Asia. (3) More recent New World movements of lineages adapted to high elevations, especially from North America into the Andes of South America over the last 5 million years. Base maps for the Eocene (≈50 million years ago) (*Upper*) and the Miocene (≈14 million years ago) (*Lower*) are based on C. R. Scotese's PALEOMAP Project (www.scotese.com). Darker gray areas show the hypothesized distribution of tropical climates during those time periods [see Fine and Ree (2006)].

opportunities, these plants maintained their tropical physiological tolerances and moved out of northern regions as climates shifted, as opposed to adapting to colder, seasonal climates and maintaining a northern distribution. The same sort of explanation, involving tropical niche conservatism, applies to other major tropical disjunctions, including subgroups within Melastomataceae (Renner *et al.*, 2001) and Lauraceae (Chanderbali *et al.*, 2001), the latter probably moving from east to west through the boreotropics [for possible additional examples see Krutzsch (1989), Lavin and Luckow (1993), Richardson *et al.* (2004), Pennington *et al.* (2006)].

A second example is in some ways a mirror image of the first. This concerns plants that were able to adapt to cold, highly seasonal environments in the north. The lineages that did manage this transition were able to move (often repeatedly and at different times) around the Northern Hemisphere, especially as a major corridor through Beringia opened and closed with fluctuating climates (Donoghue and Moore, 2003). Ultimately, these movements yielded the very common disjunctions between the temperate forests of eastern Asia and eastern North America (Wen, 1999; Milne and Abbott, 2002; Donoghue and Smith, 2004.

Here, too, it is important to appreciate the dual role played by PNC. First, recall that only some originally tropical lineages managed to make the transition to temperate climates (Latham and Ricklefs, 1993; Judd *et al.*, 1994). Malpighiales provide an example (Davis *et al.*, 2005). As noted above, Malpighiaceae remained restricted to tropical climates, and the same is true of most other major lineages within Malpighilaes. Only a few lineages made it out of the tropics and have been successful in the northern temperate zone, including violets (Violaceae), willows (Salicaceae), and St. John’s worts (Hypericaceae). As suggested above, this may relate to the complexity of the cell-level adaptations necessary to tolerate frost. Second, just as only some tropical lineages adapted to temperate climates, only some temperate plant lineages adapted to even colder climates that would have allowed their continuous distribution through Beringia, even today. It is also noteworthy that few temperate-adapted plant lineages appear to have moved back into truly tropical climates, although in this case competition may also have played an important role.

One final aspect of this case is noteworthy. There is still little phylogenetic evidence for the argument [see Latham and Ricklefs (1993)] that the majority of transitions from the tropics into the northern temperate zone took place in Asia. However, it is noteworthy that “out of Asia” biogeographic inferences have been the most commonly reported to date and appear to well outnumber originations in North America and subsequent movement to Asia (Donoghue and Smith, 2004). The continuous connection that existed in Asia between tropical and temperate climates and vegetation types throughout the Tertiary, and the great complexity of the landscape, may have promoted both the generation and the maintenance of higher species diversity in eastern Asia as compared with North America or Europe (Latham and Ricklefs, 1993; Qian and Ricklefs, 1999, 2000; Xiang *et al.*, 2004).

My third example concerns plants adapted to high-elevation alpine conditions. Historical biogeographic analyses of several clades that have succeeded in mountainous areas around the world indicate that these originated in the Northern Hemisphere, often in Asia, moved around the Northern Hemisphere, and then, much more recently, moved into South America, where they have radiated in the Andes. Valerianaceae provide an example (Bell and Donoghue, 2005; Moore and Donoghue, 2007). These plants appear to have originated in the Himalayas, to have moved to North America, and then into South America, perhaps on the order of 6 million to 8 million years ago, not long before the physical connection was established. In the Andes there are now ≈150 species of *Valeriana sensu lato*. Similar patterns of movement and diversification have been documented in *Gentianella* (von Hagen and Kadereit, 2001), *Halenia* (von Hagen and Kadereit, 2003), and *Lupinus* (Hughes and Eastwood, 2006), to name a few cases.

Two aspects of this case warrant comment. First, this pattern provides perhaps the clearest case of the movement of preadapted plants into a region as physical changes created new climates. Owing to the formation of the corridor and the dramatic rise of the Andes in the same time frame, movement into these habitats was evidently easier than the evolution of alpine adaptations *in situ*. However, it remains unclear how many resident South American plant lineages living at lower, warmer elevations, gave rise to Andean alpine plants (e.g., *Espeletia*, Asteraceae; *Puya*, Bromeliaceae). Second, it is noteworthy that a number of these movements into the Andes appear to have been accompanied by an upward shift in diversification rate. One obvious factor is geographical complexity and its promotion of allopatric speciation, at least in part as a function of PNC (Wiens, 2004). But, another important factor may have been the relative lack of occupancy by South American plants, owing in part to the relative difficulty of evolving the necessary traits *in situ*. In exploring this case further, however, it will be important to bear in mind differences between adapting to tropical highlands versus cold climates at high latitudes [see Janzen (1967) and Körner (2003, 2007)].

CONCLUDING THOUGHTS

Explanations for major patterns in the distribution of biodiversity have traditionally tended to focus on environmental correlations and local determinism. With the rapid rise of phylogenetic knowledge, a growing appreciation of the extent and possible roles of phylogenetic niche conservatism, and the development of better analytical tools, especially to infer historical biogeography [e.g., Ree *et al.* (2005)] and rates of diversification [e.g., Chan and Moore (2005) and see Ricklefs (2007a)], the stage is clearly set to reintegrate historical factors into such explanations. These are in no way meant to replace environmental explanations, but rather to complement them and connect them to the speciation, extinction, and migration processes that ultimately underlie such patterns (Wiens and Donoghue, 2004).

The argument I am making in several ways parallels the view set out by Gould and Lewontin (1979) on the study of adaptation. They argued that adaptation is caused not by the environment, but by the interaction of the environment with the evolved, organismic substrate. They viewed the substrate in this interaction as determining the outcome just as much as the environmental pressures and argued that these should be treated as equal partners in the causal explanation. Likewise, I am arguing that it is the action of changing environments on the evolved ecological characteristics of lineages that results in the patterns of biodiversity we observe today, and, furthermore, that the role that these lineages play is every bit as interesting and powerful in determining the outcome. In short, I am agreeing with Robert Ricklefs (2004) that we should "raise regional and historical factors to equal footing with local determinism in their influence on the diversity–environment relationship and geographical patterns of diversity in general." Fortunately, whereas the integration of phylogenetic knowledge into such explanations once seemed unnecessary, and for a time seemed interesting but impractical, now it seems virtually inevitable.

Finally, it is worth reflecting on the future of biodiversity in light of the basic principle highlighted here. In the deep evolutionary past, corridors for the movement of biotas within and among continents were opened or shut based primarily on the relative position of landmasses, geologic particulars (e.g., the location and orientation of rivers and mountain ranges), and climate changes. Moving into the future, anthropogenic habitat fragmentation adds a complicating new variable to the equation, as does the current rapidity of climate change and the wholesale movement of species by humans. Depending on the vagility of the organisms involved, the habitat discontinuities imposed by humans may limit the impact of the migration of preadapted species in community assembly, which I believe has played such an important role in the past. The consequences for community composition, structure, and function are unclear. One possibility is that anthropogenically isolated habitats will remain, at least for a time, "empty" of species from surrounding areas that might be well adapted to them. On the other hand, barriers to migration might create circumstances that favor niche shifts in the resident species [cf. Ackerly (2003)]. Then again, such changes would be counterbalanced by probable reductions in genetic diversity and human species introductions.

If attention is focused on ecological traits that are highly labile, and likely to evolve quite rapidly, optimism about *in situ* adjustments may well be warranted. My basic argument is that it is important to appreciate that some ecological traits are far less likely to evolve rapidly, and that this conservatism has consequences. As we proceed to predict responses to global change, I believe it will be necessary to acknowledge and more finely characterize the spectrum that exists in the evolutionary lability of ecologically relevant traits. Ironically, however, we are rapidly creating genuinely unparalleled circumstances in which it is becoming difficult to apply our expanding knowledge of the past to predict the future. In this very important sense, it is becoming increasingly unclear what lies ahead for biodiversity.

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14

Phylogenetic Trees and the Future of Mammalian Biodiversity

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Phylogenies describe the origins and history of species. However, they can also help to predict species' fates and so can be useful tools for managing the future of biodiversity. This chapter starts by sketching how phylogenetic, geographic, and trait information can be combined to elucidate present mammalian diversity patterns and how they arose. Recent diversification rates and standing diversity show different geographic patterns, indicating that cradles of diversity have moved over time. Patterns in extinction risk reflect both biological differences among mammalian lineages and differences in threat intensity among regions. Phylogenetic comparative analyses indicate that for small-bodied mammals, extinction risk is governed mostly by where the species live and the intensity of the threats, whereas for large-bodied mammals, ecological differences also play an important role. This modeling approach identifies species whose intrinsic biology renders them particularly vulnerable to increased human pressure. We outline

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how the approach might be extended to consider future trends in anthropogenic drivers, to identify likely future battlegrounds of mammalian conservation, and the likely casualties. This framework could help to highlight consequences of choosing among different future climatic and socioeconomic scenarios. We end by discussing priority-setting, showing how alternative currencies for diversity can suggest very different priorities. We argue that aiming to maximize long-term evolutionary responses is inappropriate, that conservation planning needs to consider costs as well as benefits, and that proactive conservation of largely intact systems should be part of a balanced strategy.

The Tree of Life—phylogeny—is a powerful metaphor for life's diversity, showing all species, including our own, as part of an interrelated whole. But phylogeny is more than a metaphor. It is also a research tool—the result of evolutionary processes integrated over the history of life, it can be analyzed for insights into how those processes have shaped today's biota (Harvey *et al.*, 1996). This approach is becoming increasingly powerful as the trees become ever more inclusive, built from rapidly accumulating databases using methods that continue to be improved (Bininda-Emonds, 2004; Cracraft and Donoghue, 2004).

Species' histories are of interest, but their futures are of more pressing concern. The Tree of Life is currently under sustained attack, as people increasingly dominate landscapes (Millennium Ecosystem Assessment, 2005a). Comparisons of extinction rates between today and geological history are difficult for many reasons (Jablonski, 1994), but the Tree of Life is already being pruned more quickly than it is growing (Purvis and Hector, 2000), and extinction rates are projected to rise by at least another order of magnitude over the next centuries (Mace *et al.*, 2005). This chapter describes how phylogeny has a role to play in understanding the pattern of survivors and casualties and how it can help us both to predict species' futures and to estimate some of the biodiversity value that would be lost if they went extinct.

We focus on mammals as a model system. They are much better known than almost any other group, with a mature species-level taxonomy (Wilson and Reeder, 2005), a largely complete evaluation of species' extinction risk (Baillie *et al.*, 2004), a large database of ecological, life history, and geographical information (K.E.J., J.B., A.P., C.D.L.O., S.A.F., Christina Connolly, Amber Teacher, J.L.G., R.G., Elizabeth Boakes, Michael Habib, Janna Rist, Chris Carbone, Christopher A. Plaster, O.R.P.B.-E., Janine K. Foster, Elisabeth A. Rigby, Michael J. Cutts, Samantha A. Price, Wes Sechrest, Justin O'Dell, Kamran Safi, M.C., and G.M.M., unpublished data), and a comprehensive species-level estimate of phylogeny

(Bininda-Emonds *et al.*, 2007). [Many node ages in Bininda-Emonds *et al.* (2007) were slightly affected by a software bug; all our analyses use corrected dates (Bininda-Emonds *et al.*, 2008).] As always with a model system, advantages come at a price. Mammals are atypical (e.g., they are much larger than most other species), so results from them cannot necessarily be extrapolated more broadly. However, mammals are a charismatic group of special interest to many people, so results have value even if they cannot be generalized. We start with a snapshot of present mammalian diversity and the (overwhelmingly anthropogenic) pressures that species face, before going on to describe recent and ongoing attempts to understand the present and possible future consequences of those pressures.

A SNAPSHOT OF MAMMALIAN BIODIVERSITY

Mammalian species are distributed very unevenly among genera, families, and orders (Purvis and Hector, 2000; Wilson and Reeder, 2005). Differences in age among taxa of a given rank (Avise, Chapter 15, this volume) confound evolutionary interpretation of the pattern, but the phylogeny permits a test of whether the chances of diversification have indeed varied among lineages. Under the equal-rates Markov model (ERM), in which chances are equal, phylogenies should have a weighted mean I [the degree to which species are partitioned unequally between sister clades (Purvis *et al.*, 2002)] not significantly >0.5. The estimate of phylogeny (Bininda-Emonds *et al.*, 2007) has a weighted mean I of 0.657 (SE = ±0.0131), well above 0.5 (weighted t test vs. 0.5: $t_{848} = 11.98$, $p << 0.001$), indicating that lineages have had different propensities to diversify. Such inequality is common throughout the Tree of Life (Mooers and Heard, 1997; Purvis, 1996) and prompts the search for traits that might be responsible. Phylogenetic analyses reveal that large litter size and high abundance are both linked with high richness in sister-clade comparisons pooled across four orders (primates, carnivores, marsupials, and bats), whereas small body size and short gestation period also predict high richness within carnivores (Isaac *et al.*, 2005). In common with most comparable studies on other taxa (Coyne and Orr, 2004), however, the biological traits leave most of the variance in richness unexplained, suggesting a possible role for the environment.

The geographic distribution of mammalian species is also very uneven (Fig. 14.1). Mammals follow global trends for higher tropical diversity, with a strong latitudinal diversity gradient (Fig. 14.1*a*). Within the tropics, richness seems to correlate with productivity and water–energy dynamics, peaking in Amazonia at the base of the Andes, in the Great Rift Valley in Africa (where richness exceeds 250 species per 10,000 km^2), and in an arc running from the Himalayas into southeastern Asia (Fig. 14.1*b*). These

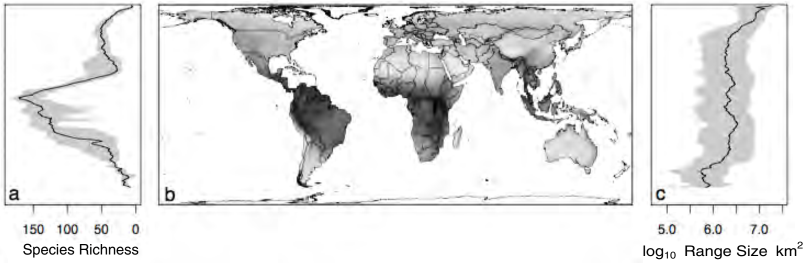

FIGURE 14.1 Geographic patterns in mammalian biodiversity. (*a*) The latitudinal gradient in species richness. The solid line shows the median; gray bands demarcate the interquartile range; species are counted in every latitudinal band (100 km north to south) in which they occur. (*b*) A map of species richness within 100 × 100-km grid cells, ranging from light (minimum = 0 species) to dark (maximum = 258 species). (*c*) The latitudinal pattern of mean geographic range size; details as for Fig. 1*a*.

peaks suggest that topographical heterogeneity has also shaped species-richness patterns (Kerr and Packer, 1997). At higher latitudes, the relationship between richness and productivity is much weaker, and ambient energy is a better predictor of richness (Kerr and Packer, 1997). The geographic pattern of mammalian richness is highly congruent with those of birds and amphibians (Grenyer *et al.*, 2006), which are also well predicted by the same environmental variables (Hawkins *et al.*, 2003; Buckley and Jetz, 2007). All these groups have many narrow-range species on the Neotropical mainland, but other "hotspots of endemicity" differ—continental shelf island systems for mammals, oceanic archipelagoes for birds, and mainland locations for amphibians (Grenyer *et al.*, 2006). The latitudinal gradient in median geographic range size in mammals (Fig. 14.1*c*) correlates strongly with the land area available within the same latitudinal bands ($r = 0.68$, although spatial autocorrelation complicates significance testing). However, median range size remains high in the northernmost bands despite the rapid decline in land area toward the Pole. Bird range sizes show similar patterns (Orme *et al.*, 2006).

The tropics have been described as an evolutionary powerhouse, acting as a "cradle" for diversity (Stebbins, 1974). Might Fig. 14.1, therefore, reflect longstanding geographic differences in diversification rates? Cradles of diversity could be of particular interest if conservation actions are to be targeted toward conserving the processes that generate diversity, a point to which we return below. The geographic pattern of recent diversification can be examined in terms of taxonomy or phylogeny, although both have their problems. Boundaries to higher taxa can be arbitrary (Avise, Chapter 15, this volume), whereas both the relative and absolute divergence times in molecular phylogenies can be controversial (Pulquério and Nichols, 2007). Because of these reservations, we use both approaches.

Taxonomically, the ratio of species to genera should indicate the regional diversification rate over the past several million years, if genera are approximately equal in age. This ratio correlates strongly with log(species richness) among equal-area grid cells (Pearson's $r = 0.61$; Fig. 14.2*a*). This correlation remains highly significant (corrected $F = 78.49$, corrected $P < 0.001$, $n = 4{,}152$: based on a subsample of cells and excluding single species occurrences) when degrees of freedom are reduced to account for spatial autocorrelation (Clifford *et al.*, 1989). Moving to phylogeny, places where a high proportion of species are on short terminal branches in the tree are likely to have rapid diversification, turnover, or immigration in their recent history (Roy and Goldberg, 2007). However, analyses are complicated by the low resolution (uncertain relationships) at the tips of the phylogeny, which introduces overestimates of the respective branch lengths. We ameliorated this problem by reducing ages of terminal polytomies using the correction suggested by Nee in Mooers and Atkins (2003) and by assuming that the descendants from each polytomy diversified under a Yule process (Nee, 2006). Fig. 14.2*b* highlights the Andean and Himalayan diversity peaks, but not the African great lakes, as recent evolutionary crucibles. Much of the temperate north stands out more than much of the tropics in this map, and there is a negative overall correlation between the proportion of short branches and log(species richness) ($r = -0.38$, corrected $F = 21.01$, corrected $P < 0.001$, $n = 4{,}210$, analyses as above), although this depended on how we corrected for terminal polytomies. This result partially echoes recent findings of higher recent speciation and extinction rates in temperate than in tropical mammals (Weir and Schluter, 2007). These maps also imply that some regions have seen marked shifts in net diversification rate, whereas others may have remained steady.

Areas of "old" and "young" diversity can be identified from the residuals of a loess regression across cells of total evolutionary history (i.e., total branch length in the phylogeny of a cell's species) on species number. The African diversity peak emerges as old, whereas much of Andean diversity is young (Fig. 14.2*c*). Character disparity—among-species variation in morphology—also shows geographic pattern: Fig. 14.2*d* maps one index of disparity, the variance in log(body mass). Disparity tends to be high where diversity is old ($r = 0.29$, corrected $F = 5.10$, corrected $P < 0.05$, $n = 4{,}210$, analyses as above), although tropical regions drive this relationship.

Mammalian biodiversity, then, shows complex geographic and phylogenetic patterns of richness, recent diversification, and character variation. The African diversity peak is old and disparate, that in Asia is young and disparate, and the Andean peak is young with low disparity. These

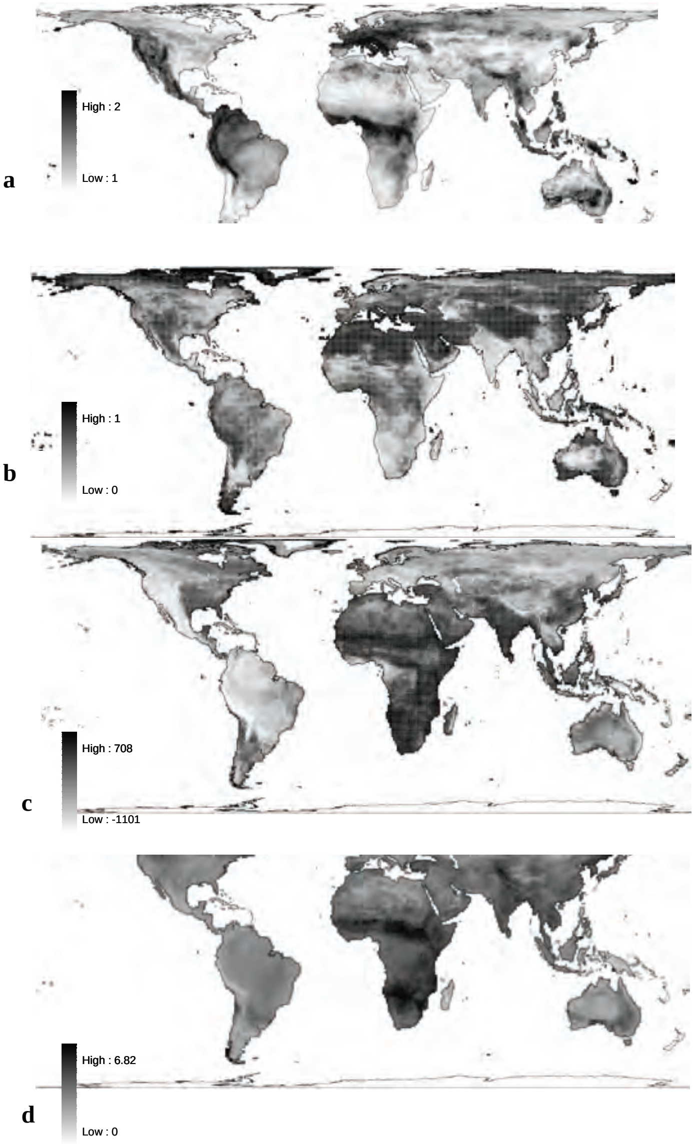

FIGURE 14.2 Maps showing four aspects of mammalian diversification and diversity. (*a*) Mean numbers of species per genus within cells. (*b*) Proportion of species with shorter terminal branch lengths than the overall median [phylogeny from Bininda-Emonds *et al.* (2007), with branch lengths corrected and modified as explained in text]. (*c*) Residuals from a loess regression of cell total evolutionary history against cell species number (phylogeny as above). (*d*) Variance in log(body mass) (unpublished data), with missing data inferred as the mean of all closest relatives with data.

patterns reflect a complex history of speciation, extinction, anagenesis, and dispersal, with each factor probably shaped by biological traits and both biotic and abiotic environmental features in ways that have changed through time. Environmental features could provide much of the missing explanation for phylogenetic asymmetry (Ricklefs, 2003), whereas traits may help to complete the explanation of geographic patterns. Other, less well known taxa doubtless have different patterns, but there is no particular reason to expect the patterns to be any simpler.

Natural diversity patterns increasingly bear the stamp of widespread anthropogenic system change. The biota we see today is already affected by anthropogenic extinction. Large, slowly reproducing mammals went extinct almost everywhere (with the notable exception of Africa, perhaps linking to the patterns in Fig. 14.2*c* and *d*) ≈7,000 to 50,000 years ago (Barnosky, Chapter 12, this volume). In the past few centuries, mammalian extinctions have mostly been on islands, notably the West Indies, with continental extinctions largely confined to Australia (Baillie *et al.*, 2004). Our analyses are therefore of an already reduced fauna. The next section considers the main ways in which human actions continue to reduce and reshape mammalian biodiversity.

THREATS FACING MAMMALIAN BIODIVERSITY

The terrestrial environment is now dominated by people—1/4 to 1/3 of the land area has been transformed for human use (Vitousek *et al.*, 1997). Additionally, human population density tends to be higher in species-rich areas, probably because productivity shapes both (Luck, 2007). Only a few mammal species fare well in human-dominated environments; the vast majority are vulnerable to the widespread and rapid anthropogenic changes. The main direct human-induced drivers that impact biodiversity now are habitat loss and fragmentation (the most important present threat), alien invasive species, overutilization, disease, pollution, and climate change (Baillie *et al.*, 2004). The International Union for Conservation of Nature (IUCN) assessed how these drivers are affecting mammals. Nearly all mammal species have been evaluated and, provided enough information was available, placed in one of the following extinction risk categories: least concern (LC), near-threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR), extinct in the wild (EW), and extinct (EX). The resulting IUCN Red List (International Union for Conservation of Nature, 2007) lists 74 mammal species as having gone extinct in their native range since A.D. 1500, 1,094 (22.5% of those evaluated) as being threatened (i.e., VU, EN, or CR), and only 2,652 (54.5%) as giving no cause for concern (i.e., as being LC).

Does extinction risk show any patterns that might help us to understand the processes affecting biodiversity loss? The "field of bullets" scenario, in which extinction strikes completely at random, is a widely used null model for extinction (Raup *et al.*, 1973; Van Valen, 1976). The metaphor comes from trench warfare, where soldiers' survival may have depended more on luck than skill. This scenario predicts that threatened species should constitute a stochastically constant fraction of any sample. Mammalian extinction risk is not a simple field of bullets but shows both geographic and phylogenetic patterns (Russell *et al.*, 1998; Mace and Balmford, 2000; Baillie *et al.*, 2004). The prevalence of risk is higher in the Old World than in the New World and higher on islands than on continents (Mace and Balmford, 2000; Baillie *et al.*, 2004). It varies among clades too, being higher than average in primates and perissodactyls and lower than average in rodents (Baillie *et al.*, 2004). Species with few close relatives are also more likely to be at risk (Russell *et al.*, 1998; Purvis *et al.*, 2000a).

These patterns reject the original field-of-bullets model, but the model lacks a geographic dimension because there may have been fields that were near to the battle but that nevertheless had no bullets. Likewise, human pressures have changed some places beyond recognition but left others almost untouched. Because closely related species often live in the same region, geographic heterogeneity in threat intensity could, by itself, cause taxonomic selectivity in extinction risk (Russell *et al.*, 1998). Alternatively, the selectivity could arise because biological differences among clades affect species' abilities to withstand threats (McKinney, 1997). How important for species' survival is staying out of the firing line, and how important is being bulletproof?

Human population density predicts proportions of threatened mammal species among continental countries (McKinney, 2001), supporting the "firing-line" model. However, an analysis of extinction risk within terrestrial World Wildlife Fund (WWF) ecoregions shows that phylogenetic nonrandomness is common within single ecoregions, where pressures may be more even than across the globe. Within each ecoregion, we generated phylogenetically independent contrasts (essentially, differences between sister clades) (Harvey and Pagel, 1991) in extinction risk (0 for LC species, 1 for species having a higher status; data-deficient and unevaluated species were excluded) on the phylogeny (with polytomies resolved arbitrarily and branch lengths set to unity) and compared the sum of the absolute values of standardized contrasts with the sums obtained from 1,000 randomizations of the risk data among the ecoregion's species. If high-risk species are strongly clumped in the phylogeny, the observed sum will be lower than in 95% of the simulations. Of 691 ecoregions with at least three higher-risk species and some variance in extinction risk, 386 (54%) showed significant clumping. Interestingly, the strength (rather

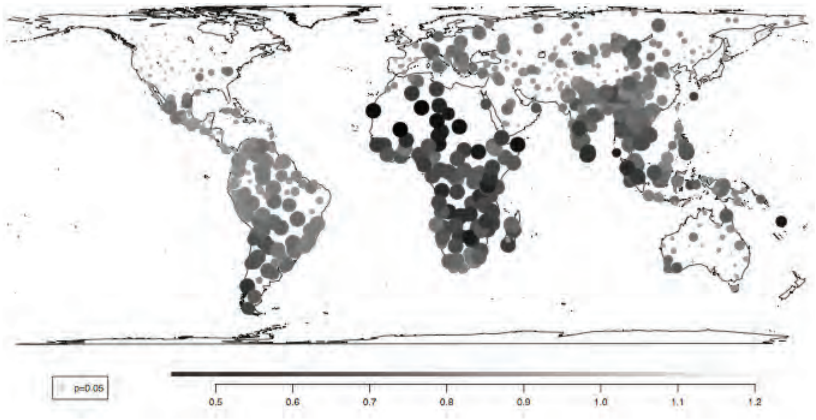

FIGURE 14.3 Strength and significance of clumping in extinction risk within WWF ecoregions. Scale bar below the map indicates clumping strength. A value of 1 indicates randomness, and clumping is stronger for lower values. Circle size indicates the p value [radius is proportional to $-\ln(p)$]; circle size for $P = 0.05$ is shown at the lower left.

than the significance) of the clumping is high in most realms apart from the Nearctic (Fig. 14.3). It also appears to be stronger in ecoregions with high disparity (Spearman's $\rho = 0.316$) and with relatively old diversity (Spearman's $\rho = 0.195$). These correlations should not be taken as evidence of a functional syndrome unless confirmed at more local scales: Some of the signal probably derives from differences among, rather than within, major biogeographic realms. The prevalence of clumping of risk implies that, faced with approximately equal pressures, species differ in their ability to persist because of lineage-specific characteristics. This finding invites a search for biological correlates of extinction risk.

COMPARATIVE ANALYSES OF MAMMALIAN EXTINCTION RISK

Perhaps the most obvious proposed risk factor for extinction is large body size. The end-Pleistocene mass extinction of mammals removed mostly large species (Barnosky, Chapter 12, this volume), and declining mammals are an order of magnitude heavier, on average, than are non-threatened species (Cardillo *et al.*, 2005). There are several possible reasons: Large-bodied species are more tempting targets than small ones for hunters; they are, on average, less abundant; and they take longer to reach sexual maturity, have smaller litters of larger offspring, and have larger individual home ranges. Narrow ecological tolerances are also a plausible risk factor—habitat specialists may be more at risk than generalists from habitat loss (Fisher and Owens, 2004). A small geographic range size may reflect narrow tolerances and increase the risk that the whole of the species' range is in the firing line. Which of these features matter most for extinction risk, and are any associations consistent across all mammals?

Cardillo *et al.* (2005) carried out the most comprehensive investigation to date. Threatened species were included only if they were on the IUCN Red List because of observed decline, to avoid autocorrelation with predictor variables. Red List status, on a 0–5 scale, was used as the response variable. Many facets of geography (including human population density), ecology, and life history were tested as predictors of extinction risk, by using phylogenetically independent contrasts. A phylogenetic approach is needed because, although extinction risk and some of the possible predictors listed above (e.g., geographic range size) do not evolve along the phylogeny's branches like, say, body size does, they nonetheless tend to show phylogenetic signal [i.e., they tend to take more similar values in close relatives than in species chosen at random; (McKinney, 1997; Purvis *et al.*, 2000b; Fisher and Owens, 2004)]. Minimum adequate models were derived from a large initial set of predictors. This approach helps exclude variables that correlate only indirectly with extinction risk, for example, because another variable shapes both them and risk.

The predictors of risk were significantly different for smaller and larger species, with the importance of many predictors changing markedly at a body size of ≈3 kg. Species smaller than this fit the firing-line model: They are more likely to be threatened if they have small geographic ranges, live in temperate areas, face high human population densities, and live where a high proportion of the other mammal species are also threatened. Larger species, however, face multiple jeopardy: Biology matters as well as geography, with high-abundance, small neonates, and many litters per year all independently helping to bullet-proof species. High abundance is predicted to bullet-proof species if the field-of-bullets model operates at the level of individuals rather than species (Erwin, 2006a), but such a model also predicts that no other biological traits would independently predict risk.

For both large and small mammals, the most important single risk factor is small geographic range size. The firing-line model predicts that small-ranged species will be most at risk because a single localized threat can impact their entire distribution. However, range size itself varies systematically among clades [although it shows weaker phylogenetic signal than, e.g., body size (Gaston, 2003; KE Jones *et al.*, 2005)], suggesting that it is shaped, at least in part, by organismal traits such as dispersal ability (Böhning-Gaese *et al.*, 2006) or niche breadth as well as by circumstances of geography. For example, small-ranged species are more common at low latitudes and within climatically stable regions. Any traits, including geographic location, that confer large species ranges also help make species bulletproof (although geographical variation in species' range sizes again complicates separation of geographical variability in threat intensity from intrinsic biological vulnerability).

Large-scale analyses can find general predictors of extinction risk but can miss interesting variation among regions or clades, which more narrowly focused models might pick up (Fisher and Owens, 2004). Order-specific models typically have higher explanatory power than the large-scale models. These models have some common features, such as the importance of geographic range size, but also differ considerably (Cardillo *et al.*, 2008). For example, body size is a predictor in bats but not in rodents, whereas different life history traits predict risk in carnivores (gestation length) and ungulates (weaning age, interlitter interval). Likewise, different environmental factors and measures of human impact are implicated in different taxa. The models also vary regionally, with life history mattering less in north temperate regions than elsewhere (Cardillo *et al.*, 2008).

One likely source of variation in models is that different drivers may select against different characteristics and show spatial variation in intensity. Broad-scale analyses may therefore lump competing signals together (Owens and Bennett, 2000). Within artiodactyls, predictors of extinction risk differ between hunted and nonhunted species: Late weaning age was the sole risk factor among the former, whereas low income levels among local people and small range size predicted risk among the latter (Price and Gittleman, 2007). More generally, low reproductive rates and large size are likely risk factors for overexploitation, but a specialized habitat may matter more under habitat loss (Owens and Bennett, 2000). Analyses focused more tightly on driver-specific responses often tend to consider far fewer species, in which case far fewer predictor variables can be considered simultaneously without overfitting, and statistical power may be lower. On the plus side, the tighter focus can reduce the chance of mixed signals [although interaction terms can also do this (Price and Gittleman, 2007)], and more precise measures of driver intensity and extinction risk might be available than can be had globally (Fisher *et al.*, 2003; Isaac and Cowlishaw, 2004). Broad- and narrow-scale analyses each give part of an obviously very complex picture. Furthermore, we have focused on phylogenetic nonindependence, but to fully consider the interaction between biology and geography, the development of methods that also deal with spatial nonindependence in comparative data will be critical.

Analyses modeling risk as a function of intrinsic biology (i.e., not including driver information) can highlight species at lower risk than expected from their geography, ecology, and life history (Cardillo *et al.*, 2006). Such species may be particularly likely to decline rapidly if drivers intensify, because their attributes are repeatedly found in rapidly declining taxa. Cardillo *et al.* (2006) termed this "latent risk" and proposed 20 regions with largely intact, but intrinsically susceptible, mammalian faunas. These include the Nearctic boreal forests and the island arc of Southeast Asia, and are mostly not exceptionally high in numbers of total, endemic, or threatened species. Many have much less than 10% of their land within reserves, and some (especially in Southeast Asia) face very rapid human population growth. As such, latent-risk hotspots might represent cost-effective options for long-term conservation. However, these analyses do not yet consider realistic scenarios of future driver patterns; rather, they implicitly assume that places with low intensity will experience an increase to more typical levels (Cardillo *et al.*, 2006). The next section discusses how more policy-relevant predictions could be obtained by projecting future driver patterns based on explicit scenarios.

MODELING FUTURE DECLINES

Predicting future declines is more complex than explaining present declines, because the future is not just a linear extrapolation from the past and present. Past extinctions were largely caused by invasive species and overexploitation; habitat alteration is now a more important driver (Baillie *et al.*, 2004). Changes in land use have been mapped historically (www.mnp.nl/hyde) and are tracked in the present day (http://glcf.umiacs.umd.edu/data), but analogous spatial data for other main drivers are more problematic. Wild species might be most vulnerable to overexploitation where people live at high density and have few other protein sources, suggesting that predictive models can be developed at regional scales (Fa *et al.*, 2003; Ling and Milner-Gulland, 2006). The patterns and driving processes behind invasive species have varied over time (Mack and Lonsdale, 2001), and, although there are clear associations with global movements from human migration and trade, identifying clear predictive methods for the intensity of invasives is a work in progress (Hastings *et al.*, 2005). The same is true for disease (Pedersen *et al.*, 2007).

Given the difficulties in obtaining spatial data on the present intensity of direct drivers, let alone future projections, an alternative is to work with information on indirect drivers—in particular, human population density and growth and patterns of land conversion. Projections of these drivers are available under a range of socioeconomic scenarios (Millennium Ecosystem Assessment, 2005b). Intensity data alone are not enough, however; the response curves linking intensity to decline are also needed, and responses will depend on how bulletproof the biota is. Thus, declines need to be modeled as a function of both driver intensity and relevant biological attributes. A first step (Cardillo *et al.*, 2004) considered a single driver (human population density) under a single growth scenario, coupling explanatory models of carnivore extinction risk from comparative analyses with human population projections to identify species whose conservation status was likely to worsen.

Here, we enlarge this approach in a preliminary analysis of two drivers and all mammals. Across ecoregions, the proportion of species with risk status higher than LC was modeled (as a binomial denominator) as a function of two drivers and two summaries of biological vulnerability by using generalized additive models (Wood, 2006) to avoid forcing any particular form on the relationship. A smooth relationship was fitted to link risk level to mean human population density (Center for International Earth Science Information Network and Centro Internacional de Agricultura Tropical, 2005) and the proportion of land converted to urban or cropland (European Commission, Joint Research Centre, 2003; Center for International Earth Science Information Network *et al.*, 2004). A second smooth relationship was fitted to control for two biotic variables [proportion of species weighing >3 kg, the size at which ecology and life history begin to influence risk strongly (Cardillo *et al.*, 2005), and the proportion of species in the lowest quartile of global range size (K.E.J., J.B., A.P., C.D.L.O., Susanne A. Fritz, Christina Connolly, Amber Teacher, J.L.G., R.G., Elizabeth Boakes, Michael Habib, Janna Rist, Chris Carbone, Christopher A. Plaster, O.R.P.B.-E., Janine K. Foster, Elisabeth A. Rigby, Michael J. Cutts, Samantha A. Price, Wes Sechrest, Justin O'Dell, Kamran Safi, M.C., and G.M.M., unpublished data)]. Fig. 14.4 shows the marginal effect of the drivers on extinction risk. The two drivers are strongly correlated across ecoregions and interact strongly. As expected, risk is low when both drivers are at the very lowest levels. However, risk rises rapidly as either driver increases. Medium levels of land conversion and low density are associated with high levels of risk, but risk falls as land conversion rises further. This suggests that land conversion is an extinction filter (Balmford, 1996), removing one set of species sufficiently thoroughly that highly converted regions can again have low levels of risk, with only the more bulletproof taxa remaining. Scenario analysis will obviously need to count projected extinctions as well as declines and may need to consider historical as well as present driver patterns. As human density reaches high levels, risk levels become uniformly higher.

A more refined model, perhaps incorporating other drivers, could be combined with projected future driver intensity to predict where a high proportion of species will decline. Such an approach uses the spatial heterogeneity in present driver intensity as a surrogate time series, with high-intensity ecoregions suggesting what will happen elsewhere as conditions deteriorate. However, incorporating climate change into this modeling approach presents major challenges. Because it has not been a major driver of present risk patterns, we have not yet seen how intensity

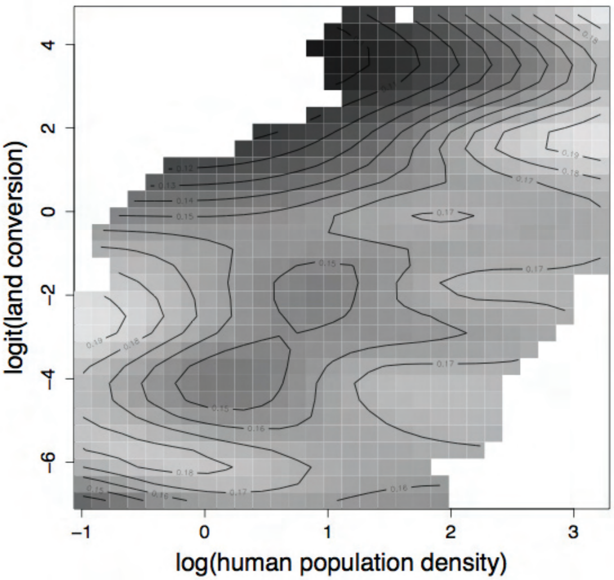

FIGURE 14.4 The surface relating the prevalence of extinction risk to urban and agricultural land use and human population density (HPD), controlling for two indices of biological susceptibility, among ecoregions. White regions in the top left and bottom right corners contain no ecoregions. Light = low risk; dark = high

will relate to impact and cannot use spatial heterogeneity as a guide. Bioclimatic envelope models suggest that climate change is already affecting many species including mammals (Parmesan and Yohe, 2003) and may soon be the dominant driver, possibly exacerbated by interactions with invasive species and other threats (Thuiller, 2007). Climate change is likely to particularly impact species that face geographical or biological barriers to dispersal or that depend on environmental cues that may break down as climate changes (Bradshaw and Holzapfel, 2006).

SETTING PRIORITIES AMONG AREAS

Conservation spending is not nearly enough to maintain even the current inadequate network of reserves and protected areas (James *et al.*, 2001). The identification and prioritization of global conservation networks are a major focus of conservation dollars (Halpern *et al.*, 2006). However, rankings inherently depend on the currency used to evaluate regions. A simple demonstration can be provided by ranking ecoregions, in this case by applying a greedy complementarity algorithm, to maximize the capture of seven possible currencies for mammalian conservation: species richness; total numbers of species extinctions predicted in the next 100 years from current Red List status [using the probabilities of extinction in Redding and Mooers (2006)]; two measures combining evolutionary uniqueness and present extinction risk [EDGE (Isaac *et al.*, 2007) and ELEH (Redding and Mooers, 2006), both summed across species in the ecoregion]; evolutionary dynamism (indexed as the sum of the reciprocal of the terminal branch lengths of species in the ecoregion); evolutionary history (estimated as the total branch length in the phylogeny of the ecoregion's species, adjusted for polytomies as described above); and total latent risk (Cardillo *et al.*, 2006). Species-rich areas are likely to sum to higher values and, hence, rank highly across all currencies. Nonetheless, Table 14.1 shows that rank order differs considerably even for similar measures designed to optimize the same currency (e.g., EDGE and ELEH). The biggest difference is between latent risk and numbers of extinctions. This is perhaps unsurprising, because latent risk gives high weights to species that are less threatened (although not all species were weighted for latent risk, weakening the comparison). A greedy algorithm makes choices based on maximizing the immediate gain in currency at each step and so may give globally suboptimal complementarity networks (Pressey *et al.*, 1996). In addition, ecoregions are, in any case, larger than most current conservation-management units (Grenyer *et al.*, 2006). Our aim here is simply to show that surrogacy among currencies may be low. Furthermore, other more subjective or hard-to-quantify criteria might also be considered important—for example, the ecological function of a species or lineage, its cultural significance, or its charismatic appeal to humans (Avise, 2005)—further impeding comparisons between areas with similar numbers of species.

Even if a currency can be agreed upon, a reserve network optimized for one clade is likely to be suboptimal for another (Grenyer *et al.*, 2006). It is often tempting to use a single group as a surrogate for biodiversity

TABLE 14.1 Numbers of Ecoregions Jointly Ranked in the Top 50 (of a Total of 791) by Each Pair of Currencies, According to Greedy Complementarity Searches

	Richness	EDGE	ELEH	Extinctions	Diversification	Latent Risk	Evolutionary History
Richness	50	41	22	21	34	15	36
EDGE		50	26	22	33	17	39
ELEH			50	34	18	10	26
Extinctions				50	20	9	21
Diversification					50	16	30
Latent risk						50	16
Evolutionary history							50

as a whole, but other clades are likely to have very different—and equally complex—patterns of diversity and extinction risk. The lack of strong surrogacy among groups introduces extra uncertainty into the measured biodiversity value of the regions being considered. In addition, we have focused on conservation benefits rather than costs, but costs vary spatially by several orders of magnitude (Balmford *et al.*, 2003a; Halpern *et al.*, 2006). Cost–benefit models can suggest very different priorities from allocations based solely on perceived biodiversity value (Possingham *et al.*, 2002). So, if we assume that rational decision making must consider both benefits and costs, perhaps the most sensible investment would be in intact but susceptible regions (Balmford *et al.*, 2003a; Cardillo *et al.*, 2006). Public health-care systems may provide a useful analogy: A balanced health-care strategy includes money for preventative medicine as well as for hospital wards and life support.

BEYOND THE DECLINES: THE EVOLUTIONARY FUTURE?

The primary goal for most conservation management has been to maximize preservation of current diversity. However, by altering the environment, humans also influence future evolution (Smith and Bernatchez, 2008). A previous National Academy of Sciences Colloquium (Cowling and Pressey, 2001; Myers and Knoll, 2001) raised an important question: Should conservation goals be extended to consider the evolutionary future? A range of timescales might be considered. In the short term, species-recovery plans can address the requirements needed for continued adaptive evolution within populations (Mace and Purvis, 2008). But what of the longer term? We can identify clades that have recently diversified and the regions in which they are found (Fig. 14.2*b*). These lineages or areas might represent engines of speciation: Are they therefore conservation priorities? The distinction between maximizing evolutionary history versus centers of diversification is nontrivial. A network of reserves designed to capture maximal evolutionary history would look very different from one designed to capture rapidly speciating lineages (Table 14.1), because rapid diversification results in low phylogenetic diversity per species (Mace *et al.*, 2003; Roy and Goldberg, 2007). However, past "success" may be a poor indicator of future performance because of the contingent nature of evolution (de Queiroz, 2002; Mace *et al.*, 2003). The geographic pattern of mammalian diversification rates has changed markedly through time (Fig. 14.2*a*–*c*), and different lineages have also radiated at different times (Alroy, 2000; Bininda-Emonds *et al.*, 2007).

One secure prediction is that future environmental conditions will almost certainly differ from those in the past. Nonetheless, extrapolating current trends, key environmental changes are likely to include increasing habitat loss and fragmentation, drastic shifts in species abundances and distributions, and climate change (see above) (Myers and Knoll, 2001; Barraclough and Davies, 2005). Changes in the biotic and abiotic composition of the environment (including extinctions) may restructure niche space and moderate constraints on diversification imposed by niche saturation. Major turnovers in species composition may therefore be expected (Tilman and Lehman, 2001). Unfortunately, we lack detailed information on the past states of these attributes in geological history and so cannot easily construct quantitative empirical models that can be projected forward. Predicting the evolutionary future is hampered by large uncertainty about the magnitude and form of environmental change and by lineage-specific responses. If we wished to safeguard the evolutionary future, a sensible strategy would be to maintain a set of species that is overdispersed with respect to their ecological adaptations and (as a simple proxy) their phylogeny, maximizing the possibility of having the right set of features in an uncertain future (Crozier, 1997).

Returning to our original question, should conservation goals consider the long-term evolutionary future? We sound two notes of caution. First, although we have restricted our focus to mammals, they are only a tiny branch on the Tree of Life, and many of the major limbs, from ciliates to *Chlamydia*, may be better insulated from anthropogenic disturbances (Nee, 2005). The evolutionary future of life on Earth is therefore unlikely to be in serious jeopardy. Second, anthropogenic environmental change and extinctions are occurring on the order of tens to hundreds of years, but times to speciation are frequently estimated in thousands to millions of years (Barraclough and Davies, 2005), and recovery times after previous mass extinction events were perhaps 5–10 million years (Erwin, 2001). These timescales are too great for practical management. Diversity will almost certainly rebound after the current extinction event; however, it may be composed of species descended from a different, as yet unknown, subset of lineages from those that dominate now, and humans will likely not be included among them. Practical conservation should retain its focus on minimizing declines and extinctions in the present day.

ACKNOWLEDGMENTS

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15

Three Ambitious (and Rather Unorthodox) Assignments for the Field of Biodiversity Genetics

JOHN C. AVISE

The field of molecular genetics has many roles in biodiversity assessment and conservation. I summarize three of those standard roles and propose logical extensions of each. First, many biologists suppose that a comprehensive picture of the Tree of Life will soon emerge from multilocus DNA sequence data interpreted in concert with fossils and other evidence. If nonreticulate trees are indeed valid metaphors for life's history, then a well-dated global phylogeny will offer an opportunity to erect a universally standardized scheme of biological classification. If life's history proves to be somewhat reticulate, a web-like phylogenetic pattern should become evident and will offer opportunities to reevaluate the fundamental nature of evolutionary processes. Second, extensive networks of wildlife sanctuaries offer some hope for shepherding appreciable biodiversity through the ongoing extinction crisis, and molecular genetics can assist in park design by helping to identify key species, historically important biotic areas, and biodiversity hotspots. An opportunity centers on the concept of Pleistocene Parks that could protect "legacy biotas" in much the same way that traditional national parks preserve special geological features and historical landmarks honor legacy events in human affairs. Third, genetic perspectives have become an integral part of many focused conservation efforts by unveiling ecological, behavioral, or evolutionary phenomena relevant to

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population management. They also can open opportunities to educate the public about the many intellectual gifts and aesthetic marvels of the natural world.

Creationis telluris est gloria Dei ex opere Naturae (The Earth's creation is the glory of God as seen in Nature's works).

Carolus Linnaeus, preface to *Systema Naturae*

In the 1700s, Carolus Linnaeus (1759) devised a hierarchical system to rank and classify organisms. He did so without knowledge of evolution, presuming instead that static species (albeit modified occasionally by hybridization) had been present since the time of Creation. A century later, Charles Darwin (1859) identified natural selection as a creative but natural agent of adaptive evolution. He did so without a proper understanding of genetics, sometimes presuming that heredity involved miscible gemmules in the blood. Nearly a century later, in the mid-1900s, Aldo Leopold (1949) crafted a powerful environmental ethic based on ecological considerations. The extraordinary accomplishments of these three great scientists illustrate that systematics, evolutionary biology, and conservation science—three cornerstones of modern biodiversity research—can be (and often have been) practiced successfully without material input from the field of genetics. This is ironic because, fundamentally, evolution is genetic alteration through time, biodiversity is genetic diversity (including epigenetic and emergent phenomena), and nature's genetic diversity is what is being depleted in the current extinction crisis that has spurred the conservation movement.

A growing awareness of genetic operations and principles, beginning with the findings of Gregor Mendel (a younger contemporary of Darwin), contributed hugely to the "modern evolutionary synthesis" in the mid-1900s (Dobzhansky, 1937; Mayr, 1942; Stebbins, 1950). Nevertheless, until the 1960s at least, organismal phenotypes (such as various morphological and behavioral traits) continued to provide the vast majority of empirical data for biodiversity research. Only in the last half-century have biologists gained extensive direct access to the hereditary information embedded in the molecular structures of nucleic acids and proteins (Hillis *et al.*, 1996; Avise, 2004). What have these molecular genetic data added to the evolutionary synthesis and to conservation efforts?

Much of the molecular revolution in evolutionary biology has focused on mechanistic connections between genotype and phenotype, i.e., on attempts to understand "the genetic basis of evolutionary change" (Lewontin, 1974). In particular, a relatively young but burgeoning field known as evolution-development (''evo-devo'') addresses how the evolving genomes of diverse taxa are epigenetically modified and otherwise regulated during ontogeny to yield particular organismal phenotypes, including complex adaptations (Carroll *et al.*, 2004; Avise and Ayala, 2007). The evo-devo paradigm will continue to motivate scientific interest and generate vast research opportunities for the foreseeable future.

Here, I discuss three other areas of opportunity for molecular genetics in evolutionary biology, specifically in the realms of phylogenetics and conservation. For each of these three topics in a discipline that I call ''biodiversity genetics,'' I first summarize conventional wisdom, but then I intend to be provocative by raising scientific proposals that currently are far from mainstream but nevertheless have the potential to invigorate and perhaps even reshape the biodiversity sciences.

TREE OF LIFE

Background

Legions of biologists are currently gathering extensive molecular genetic data as part of a grand collective effort to reconstruct, once and for all, the history of life on Earth (Cracraft and Donoghue, 2004). Guiding this endeavor is the powerful conceptual metaphor of a phylogenetic tree, popularized by Ernst Haeckel in 1866. Within the next decade or two, major branches and numerous twigs in the Tree of Life will be reconstructed (nearly as accurately as may ever become possible given the finite size of genomes and the relative ease by which DNA sequence data can now be gathered). The Tree of Life project will have completed its initial descriptive mission when it enters a more mature phase in which the gains in phylogenetic understanding about species' relationships, per unit of sequencing effort, will gradually diminish.

In the meantime, goals of the exuberant young Tree of Life initiative are to estimate not only branch topologies but also the evolutionary dates of various internal nodes (Hedges and Kumar, in press). Molecular ''clocks'' will play a key role. Rates of DNA sequence evolution are known to be highly variable across lineages and loci (Li, 1997), but experience indicates that when clocks are carefully calibrated and the dates they imply are compiled across dozens or even hundreds of unlinked loci, approximate origination times can be recovered for particular clades (Kumar and Hedges, 1998; Kumar, 2005). The calibrations normally require secure temporal reference points from independent evidence, e.g., from paleontology or biogeography. Thus, estimating absolute dates as well as branch topologies in phylogenetic trees is inherently an integrative endeavor that should engage many of the biodiversity sciences.

The Tree of Life project *per se* will be much like the Human Genome project, merely the first step in a vastly broader research agenda. The complete nucleotide sequence of a human genome provided a foundation for investigating genomic operations more deeply, such as enabling geneticists to map and characterize the structures and functions of genes responsible for particular phenotypes. Analogously, a robust Tree of Life will provide a foundation for delving much deeper into nature's evolutionary operations, such as enabling phylogeneticists to map the origins and evolutionary transitions among particular organismal phenotypes or document instances of reticulate evolution (Avise, 2006). All of these sentiments are simply conventional wisdom.

I suggest that either of two polar-opposite patterns (or more likely some mixture of the two) could emerge from the Tree of Life project and that either outcome would offer its own unprecedented grand opportunity for the field of evolutionary biology. One possibility is that the tree metaphor will apply well to many or most taxonomic groups, in which case an opportunity (described later) would arise for the field of systematics. Alternatively, the tree metaphor may prove to be inadequate, and an anastomose web or network of life would better describe the histories of descent of many taxa. Several recent authors have argued that genetic exchanges across lineages, via endosymbiotic mergers and lateral DNA transfers especially in microbes (Doolittle, 1999; Margulis and Sagan, 2002; Arnold, 2006) or via hybridization in metazoan plants and animals (Arnold, 1997), have played important evolutionary roles. For example, McCarthy (2008) builds a case that new species seldom arise from the standard population genetic processes of gradual divergence via mutation, drift, and selection in allopatry, but instead that novel life forms often originate via the genetic stabilization of recombinant lineages following hybridization events (Fig. 15.1). If this hypothesis is correct, the ramifications for many areas of evolutionary biology would be profound (as described later).

Deciding whether the tree metaphor or the network metaphor better explains the history of life is a stiff challenge requiring detailed and critical appraisals of empirical evidence for many taxonomic groups. But the two hypotheses do have several distinct predictions. In terms of genealogical expectations, for example, the Tree of Life model predicts that gene trees should be topologically concordant with one another and with the species tree they compose [barring potential complications such as insufficient resolution, hemiplasy (idiosyncratic lineage sorting across successive nodes in a species phylogeny) (Avise and Robinson, 2008), and homoplasy]. In contrast, the network of life model predicts that multiple gene trees in a given taxonomic group will often be qualitatively

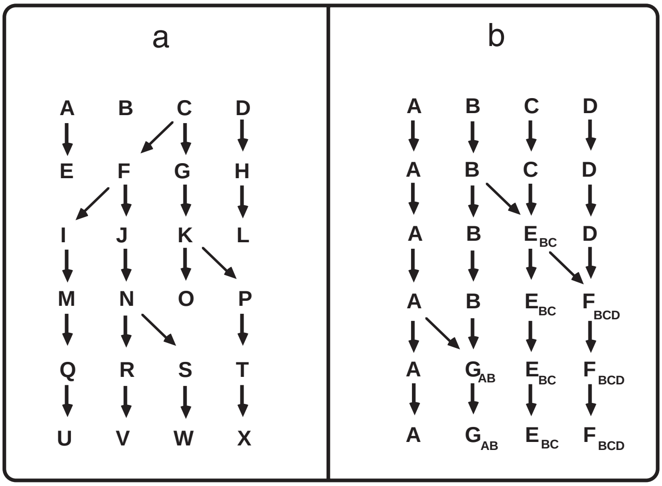

FIGURE 15.1 Simplified depictions of two competing hypotheses about the genetic history of life. (*a*) The tree model characteristic of traditional phylogenetic thought. (*b*) An example of a network model [as advanced by McCarthy (2008) in the context of hybridization and stabilization of recombinant genotypes]. Uppercase letters indicate different species or phenotypically recognizable life forms, arrows indicate historical pathways of descent, and successively lower rows in the diagrams represent more recent horizons in evolutionary time. When viewed backward in time, lineages shrink or coalesce to particular ancestors in a tree, but they expand to multiple ancestors in a network (because each new species is of hybrid origin).

discordant with one another (even after factoring out the complications of homoplasy and hemiplasy) because different DNA sequences may genuinely have highly distinct organismal histories. In evaluating the evidence, biologists must keep an initial open mind with regard to the network model because, under the competing tree model, a subtle danger exists of circular logic: Any comparative dataset can be used to reconstruct a phylogenetic tree when a tree provides the suppositional metaphor for the data analysis. Even inanimate entities (such as different kinds of chairs or cars) can be grouped into tree-like depictions based on their similarities or differences.

Depending on which evolutionary metaphor (branched genealogical trees or anastomose networks) proves generally correct for life's history, important but entirely different assignments will then emerge for the next generation of evolutionary biologists.

Assignment Given the Tree Model: Develop a Standardized Classification Scheme

The two basic functions of biological taxonomy are to (*i*) provide a universal system for information storage and retrieval, and (*ii*) encapsulate an evolutionary interpretation of biological diversity (Mayr, 1982). Unfortunately, current biological classifications are grossly nonstandardized because: (*i*) the species in named taxa are typically united by some unspecified mix of similarity by resemblance and similarity by descent, and (*ii*) even when the nested taxonomic ranks in a Linnaean hierarchy do register bona-fide nested clades the rankings remain noncomparable across different kinds of organisms (because no serious attempt has ever been made to normalize assayed characters, equilibrate taxonomic assignments, or even adopt any standardized criteria for taxonomic ranking). For example, some taxonomic genera such as *Drosophila* are an order of magnitude older than others such as *Gorilla* or *Pan*, and, because of an apples-versus-oranges problem, a taxonomic rank (such as a genus) shared by fruit flies and primates implies nothing about whether such taxa are similar with respect to genetic, phenotypic, or any other aspect of evolutionary diversity. As noted by de Queiroz and Gauthier (1992), "No scientific enterprise, least of all one that considers the promotion of nomenclatural universality as one of its primary objectives, can accept the inconsistencies and ambiguities current in biological taxonomy." Or as phrased by Hennig (1966), "If systematics is to be a science it must bow to the self-evident requirement that objects to which the same label is given must be comparable in some way."

This state of affairs could, in principle, be rectified if systematists were to adopt absolute geological time as *the* universal evolutionary yardstick against which to standardize taxonomic assignments for extant clades of known age. The basic idea, proposed by Hennig (1966) and elaborated by Avise and Johns (1999), is that extant species that separated from a common ancestor in a specified window of evolutionary time would be assigned a taxonomic rank defined by that temporal band. The boundaries of the temporal windows are arbitrary at the outset and must be ratified by convention, but a proposal that I favor in principle would link each taxonomic rank to a specific geological episode. Serendipitously, there are 17 supraspecific ranks in modern versions of the Linnaean hierarchy (Mayr and Ashlock, 1991) and also 17 primary subdivisions in the traditional geological timescale (Futuyma, 1998), thus affording the possibility of a perfect one-to-one allocation of taxonomic rank to geological episode (Fig. 15.2).

If the field of systematics from its outset had been able to implement a temporal-banding strategy for erecting biological classifications, many of the inconsistencies and ambiguities in current taxonomies could have

geological episode	taxonomic rank	mya	timeclip
Pleistocene	subgenus	0-2	**[B:pl]**
Pliocene	genus	2-5	**[C:pc]**
Miocene	tribe	5-24	**[D:mi]**
Oligocene	subfamily	24-33	**[E:ol]**
Eocene	family	33-56	**[F:eo]**
Paleocene	superfamily	56-65	**[G:pa]**
Cretaceous	suborder	65-145	**[H:cr]**
Jurassic	order	145-205	**[I:ju]**
Triassic	superorder	205-250	**[J:tr]**
Permian	cohort	250-290	**[K:pe]**
Carboniferous	subclass	290-350	**[L:cb]**
Devonian	class	350-410	**[M:dv]**
Silurian	superclass	410-440	**[N:si]**
Ordovician	subphylum	440-500	**[O:od]**
Cambrian	phylum	500-550	**[P:ca]**
Proterozoic	kingdom	550-2500	**[Q:pr]**
Archaean	domain	2500-3600	**[R:ar]**

FIGURE 15.2 Examples of how a strategy of temporal banding might be used to standardize biological classifications for extant species (see text). Shown is the one-to-one correspondence possible between 17 standard taxonomic ranks in some modern versions of the Linnaean hierarchy [see Mayr and Ashlock (1991)] and the temporal bands (Mya) for 17 traditionally recognized geological episodes [see Futuyma (1998)]. In one temporal-banding proposal, current classifications and nomenclatures could be revised (perhaps drastically), such that each clade would be ranked and named strictly according to the temporal window in which it arose. Under a less drastic proposal (which I favor), current classifications and nomenclatures would be retained, but each existing taxonomic name would simply be appended with a time clip signifying the approximate date of that taxon's origination. Note that these temporal-banding proposals do not extend to species-level taxonomic assignments, where biological criteria, including reproductive isolation (regardless of a species' date of evolutionary origin), would continue to apply.

been avoided. But formal biological names and classifications have their own historical legacies that cannot be ignored, and taxonomic stability also is highly important in systematics. One way to circumvent name changes and yet still implement the temporal-banding philosophy would be to attach a time clip (Fig. 15.2) to each extant taxon for which a reliable date of origin has been established from molecular-genetic or other evidence (Avise and Mitchell, 2007). For example, the familiar generic names *Drosophila* and *Pan* could be retained and merely time-clipped (with F:eo and C:pc) to signify their highly different evolutionary ages. Extant taxa for which origination dates remain unknown would lack time clips, but this too would convey important information by notifying the reader that a taxon's evolutionary age might be a worthy topic for additional investigation. After time clips become available for many organismal groups, it would be a simple matter for anyone to identify, sort, and compare even disparate kinds of taxa according to their approximate dates of evolutionary origin.

A temporal-banding scheme (especially as implemented in the time-clip format) could offer systematics and the biodiversity sciences several substantial benefits [elaborated in Avise and Johns (1999) and Avise and Mitchell (2007)]. It would standardize biological classifications and thereby dramatically increase their comparative information content. It would both foster and facilitate comparisons of evolutionary rates in numerous genetic and phenotypic attributes (because absolute time is the denominator in any rate equation, and the time-clipped taxon names would specify approximate dates of clade origin). It would retain the well-established Linnaean ranking system, including familiar taxonomic names, yet simultaneously enable systematists to incorporate substantive new phylogenetic knowledge, as it becomes available, into a biological classification. It would promote the often neglected notion that every phylogenetic tree has a temporal as well as a cladistic dimension and that both are important subjects for investigation. It should engage and foster collaborations among many of the biodiversity sciences in a community-wide phylogenetic mission to chart and interpret the temporal as well as cladogenetic dimensions of the planet's evolutionary heritage.

Assignment Given the Network Model: Reconsider the Nature of Evolutionary Processes

If the network model (e.g., Fig. 15.1*b*) proves to be more nearly correct for many taxonomic groups, then the challenges for systematics and evolutionary biology will be entirely different (McCarthy, 2008). First, phylogeneticists would have to admit that their dream of reconstructing a branched tree of life had been merely a pipedream, and they would have to accept the new and probably far more difficult challenge of working out the precise history of reticulation events for each organismal group and how such reticulate genealogical histories have idiosyncratically distributed particular bits and pieces of DNA from disparate sources to extant taxa. Traditional concepts of species, phylogeny, ancestry, and classification, as well as the significance of reproductive isolation, would all have to be reevaluated. Biologists would have to embrace the notion that biological processes falling somewhat outside the standard neo-Darwinian paradigm for speciation (such as interspecific hybridization and the reproductive stabilization of genetic-recombinant derivatives) could play major and previously underappreciated roles in evolution. They would have to reevaluate the origins of genetic variation on which natural selection acts and how novel phenotypic adaptations and different forms of life mechanistically come into being. In short, major shifts in evolutionary thought would be required, and this would open wonderful opportunities for the eventual emergence of a grandly updated evolutionary synthesis, 21st-century style.

PLEISTOCENE PARKS

> . . . suppose that the United States and the other leading developed countries could agree on a regular allocation for global biodiversity protection so that billions of dollars, rather than millions, could annually flow into parks and park protection. What then?
>
> John Terborgh (1999)

Background

In an eloquent requiem for nature, Terborgh (1999) has argued that, in the face of a globally burgeoning human population, the only credible prospect for preserving substantial biodiversity will be for governments [or other entities such as nongovernmental organizations (NGOs)] to set aside extensive nature sanctuaries and then actively protect those parklands in perpetuity. Many countries, including the United States, have long-established systems of National Parks that usually feature special landscapes and geological formations (such as the picturesque rocky shores of Acadia Park in Maine, the majestic mountains of Glacier Park in Montana, or the special volcanic features of Yellowstone Park in Wyoming). A growing realization is that analogous and extensive reserve systems across the globe also are urgently needed to offer explicit protection for the biological world’s special features, such as endangered species, distinctive biotic communities and ecosystems, and biodiversity ‘‘hotspots’’ (Myers, 1990; Reid, 1998).

Accordingly, many scientists and conservation organizations are actively engaged in identifying threatened sites around the world where exceptional concentrations of rare or endemic species still exist and where conservation efforts might therefore be focused to best effect (Prendergast *et al.*, 1993; Myers *et al.*, 2000; Williams *et al.*, 1996). For example, it has been estimated that as many as 44% of vascular plant species and 35% of all vertebrate species (exclusive of fishes) are confined to 25 biodiversity hotspots that comprise only 1.4% of Earth's land surface, and that for the cost of perhaps as little as $500 million annually, a biotic reserve system centered on such treasure-rich locations could be a "silver bullet" for biodiversity protection (Myers *et al.*, 2000). A related suggestion is that sites meriting high priority for protection should display exceptional concentrations of phylogenetically distinctive taxa (Vane-Wright *et al.*, 1991; Faith, 1992a; Krajewski, 1994; Humphries *et al.*, 1995; Crozier, 1997), the rationale being that organismal lineages with long-independent evolutionary histories contain disproportionately large fractions of the planet's total extant genomic biodiversity (May, 1990b, 1994; Avise, 2005).

These various suggestions for biotic reserves need not be at odds. Indeed, given the dire prospects for global biodiversity in the ongoing extinction crisis and the total inadequacy to date of commensurate responses by most governments, the more natural parklands that societies can be persuaded to sequester under any reasonable biological motivation, the better. Furthermore, the parkland effort need not be confined to governmental initiatives, as well illustrated by the welcome activities of NGOs such as the Nature Conservancy and Conservation International. A related hope is that philanthropists and profit industries also will become increasingly persuaded of the urgency to protect remaining nature, if for no other reason than in their own enlightened financial (as well as ethical) self-interest.

To pick just one such example of the potential for private involvement, an inspirational business venture ("IQ RESORTS by PANGEA WORLD") spearheaded by Hana Ayala (Lempinen, 2006) aims to partner responsible and forward-thinking members of the hotel/tourism industry with world-class scientists in a global vision to promote science and protect biodiversity as an integral part of the business plan (which would include the acquisition and preservation of extensive nature reserves in key locations, as well as the generation of new funding mechanisms for the biodiversity sciences). Three underlying premises of this initiative are as follows: (*i*) knowledge mobilized through scientific research is the ultimate inexhaustible resource; (*ii*) the world's most spectacular and biodiverse landscapes and seascapes are primary reservoirs for scientific knowledge that in turn can promote long-term conservation efforts in pragmatically effective and economically sustainable ways; and (*iii*) the international hotel industry—with its collective global ambition and growing emphasis on mind-stimulating travel experiences—has perhaps more financial interest, capacity, and incentive than any other private industry to partner with science in charting and protecting the world's premier biological heritage reserves. The PANGEA initiative aims to go well beyond traditional nature-tourism ventures by envisioning a global archipelago of interconnected "wonder sites" where the scientific study and preservation of nature are the explicit and formal motivation for linking sustainable economics with science.

The perspectives and data of ecological and evolutionary genetics can contribute to parkland conservation efforts in many ways. For example, they can help to identify species and biodiversity hotspots, especially for otherwise poorly known taxonomic groups. They can vastly improve our understanding of phylogenetic relationships of numerous taxa within and among the extant regional biotas that conservationists might seek to protect (Avise, 2004; Purvis *et al.*, 2005b; Godfray, 2007). Finally, they can help to illuminate many management-relevant aspects of the biology and natural history of particular species that warrant special conservation concern.

Most of the general sentiments summarized above (a notable exception perhaps being the PANGEA WORLD initiative) reflect conventional wisdoms, at least among many biologists. Here I suggest how phylogeographic perspectives might offer an additional opportunity in parkland motivation that is less widely appreciated. Phylogeography is a relatively young biological field that deals with descriptions and interpretations of the spatial distributions of genealogical lineages, especially within and among closely related species (Avise, 2000). An emerging phylogeographic generality is that many, if not most, extant taxonomic species are spatially subdivided into small numbers of highly distinctive historical units (Avise and Walker, 1999).

Many of these distinctive genealogical entities [sometimes referred to as evolutionarily significant units (ESUs)] (Ryder, 1986; Moritz, 1994) began diverging from one another in unglaciated biological refugia of the Pleistocene Epoch or earlier (Klicka and Zink, 1997; Avise and Walker, 1998; Avise *et al.*, 1998). In Europe, for example, extant populations of many plant and animal species bear the genomic footprints of phylogeographic differentiation in several disjunct ice-free areas (notably the Iberian Peninsula, the Italian Peninsula, and the Balkans) typically followed by post-Pleistocene dispersal from one or more of these ancestral homelands (Hewitt, 1996; Schmitt, 2007; Weiss and Ferrand, 2007). Likewise, key genealogical separations presumably tracing back to historical refugia distinguish regional populations of many species in different sections of the eastern United States (Avise, 1992; Soltis *et al.*, 2006). Qualitatively similar patterns also have been uncovered in comparative phylogeographic surveys of regional biotas in several other parts of the world (Bermingham and Moritz, 1998; Avise, 2000). In at least several cases, the current boundaries between ESUs tend to be spatially concordant with transition zones between zoogeographic provinces as identified by more traditional evidence (such as species' ranges and faunal distributions). Such concordance suggests that similar types of evolutionary forces [perhaps operating as detailed in Avise (2000)] may be responsible for both of these seemingly unrelated biogeographic phenomena.

Assignment: Identify and Preserve Nature's Recent Historical Legacies

The phylogeographic observations discussed above suggest that a concept—of Pleistocene Parks or Phylogeographic Sanctuaries—might be added to the compelling list of scientific rationales for earmarking particular regional nature reserves. Such nature reserves (like those based on traditional biodiversity hotspots) would protect and highlight the distinctive "legacy biotas" they contain, in much the same way that traditional historical landmarks (such as Civil War battlegrounds) honor important legacy events in human affairs. A carefully designed archipelago or network of phylogeographic reserves on each continent and in each marine region could thus add an emotive element of historical legacy to the catalog of societal inducements to preserve biodiversity. Furthermore, a widely promoted concept of Pleistocene Parks (like the evocative notion of Jurassic Park) might resonate well with the public and policymakers. It also might dovetail nicely with the PANGEA WORLD initiative discussed above and perhaps also with proposals to "re-wild" ecosystems with Pleistocene-like biotas (Martin, 2005).

Thus, a compelling assignment for the field of comparative phylogeography will be to map the spatial and temporal dimensions of Earth's remaining genealogical capital on all of the world's continents and ocean regions (a task already well initiated in several areas, such as Europe and parts of North America). A comprehensive phylogeographic inventory of Earth's microevolutionary history will complement ongoing attempts to identify and catalog all extant species [see Blackmore (2002)], and it also will complement ongoing appraisals of Earth's macroevolutionary history in the Tree of Life project. An overarching practical mission will be to incorporate information from all of these integrative endeavors into meaningful conservation plans, notably with regard to implementing the concept of regional sanctuaries for nature (Moritz and Faith, 1998).

BIODIVERSITY EDUCATION

> Ultimately, nature and biodiversity must be conserved for their own sakes, not because they have present utilitarian value . . . the fundamental arguments for conserving nature must be spiritual and aesthetic, motivated by feelings that well up from our deepest beings.
>
> John Terborgh (1999)

Background

"Conservation genetics" has become a popular discipline, as evidenced, for example, by two edited compilations (Loeschcke *et al.*, 1994; Avise and Hamrick, 1996), a teaching textbook (Frankham *et al.*, 2002), and a scientific journal (initiated in 2001), all bearing within their titles that exact two-word phrase. Historically, the field was associated mostly with studies of inbreeding depression and the loss of heterozygosity in small populations, but its purview has expanded greatly in recent years to include a wide range of empirical and theoretical studies that basically attempt to illuminate how patterns of genetic diversity are distributed within and among individuals, kinship groups, populations, species, and supraspecific taxa (Avise, in press). Such investigations (typically using molecular markers) routinely include genetic appraisals of the following: plant and animal mating systems, behaviors, and natural histories; magnitudes and patterns of population structure due to past and present demographic factors; gene flow, genetic drift, and various categories of natural selection; other evolutionary phenomena such as patterns and processes of speciation, hybridization, introgression, and phylogenetics; forensic analyses of wildlife and wildlife products; and many additional genetic topics that are often highly germane to the principles and the practice of conservation biology.

All of these sentiments are standard wisdom among modern biologists. So too is the realization that a strong societal preference exists for saving species that are large, attractive, or emotionally evocative, compared with those that are small, drab, or unobtrusive. Almost inevitably, conservation efforts thus become biased toward "charismatic megabiota" (Clark and May, 2002). I suggest another role for conservation genetics that is somewhat more amorphous, but nevertheless has a huge potential to elicit additional public support for meaningful societal action on behalf of nature and biodiversity protection. I am referring to a compelling educational mission: to enthuse students of all ages, including the general public as well as political, social, and religious leaders, about nature's countless underappreciated marvels.

Nearly all creatures (including the "charismatically challenged") have fascinating natural-history stories to tell, and scientists as well as natural theologians for centuries have delved into nature's workings through field observations and phenotypic investigations. Yet before the advent and widespread use of molecular markers, many of nature's incredible operations remained hidden from view. Nature can now be revealed at and through this new window of molecular-level observation, and the results are often far more engrossing than might ever have been predicted.

First are the astounding findings about genomes. Even a few years ago, few scientists could have imagined that genes encoding functional RNA and protein molecules of obvious benefit to the organism would prove to constitute only a small fraction of the eukaryotic genome, and that the rest of the composite DNA sequence includes an astonishing collection of noncoding regions, regulatory modules, pseudogenes, and legions of repetitive elements, many of which are descended from selfish virus-like elements that have proliferated and jumped around the genome often at the immediate fitness expense of their hosts. A new metaphor is emerging in which each eukaryotic genome can be viewed, in effect, as a miniature ecological community whose quasi-independent members (unlinked DNA sequences) all struggle for representation in the next generation of sexual reproducers and thereby become involved in elaborate coevolutionary games that can be quite analogous to the parasitisms, commensalisms, and mutualisms routinely observed among species in natural ecosystems (Avise, 2001). This metaphor of the genome as a submicroscopic community of genes constantly undergoing evolutionary adjustments is far from perfect, but it does promote a perspective on genomic operations that today may be much more useful and research-stimulating than earlier genomic metaphors (such as the "beads on a string" image of functional and fully collaborative genes packed tightly along chromosomes).

A second arena in which molecular genetic markers are having a huge scientific impact is in uncovering heretofore hidden secrets about the ecologies, behaviors, natural histories, and evolution of organisms in nature. An adequate discussion of this topic is far beyond the scope of this chapter, so what follow are merely a few examples of the many types of questions that scientists have answered using molecular markers, but that for one logistical reason or another had been inadequately addressed by earlier field observations or phenotypic assessments. For fuller answers to the following questions and many others like them, all in layperson language, see Avise (2002, 2006).

How big and old can natural clones of mushrooms become? (Living members of one clone were estimated to weigh a collective 100 tons, occupy 40 acres, and derive from a single zygote that formed ≈1,500 years ago.) Does each female green turtle (a highly migratory marine species) return to her natal beach to nest? (Yes, normally.) Why do female roly-poly pill bugs often greatly outnumber males? (Because many strains are infected by intracellular parasitic bacteria that are maternally transmitted and, accordingly, have evolved the physiological capability to transform male roly-polys into functional females.) Does a pregnant male pipefish or seahorse often carry a brood of offspring from more than one dam? (In some species, yes; in other cases, no.) What fraction of embryos in the nests of bluegill sunfish are foster progeny attributable to cuckoldry by sneaker males? (Approximately 20% in one well-studied population.) Did the bipedal hop arise once or multiple times in kangaroos' evolution? (Probably once only, according to phylogenetic analysis.) Why do king crabs have an asymmetrically twisted abdomen? (Because this trait appears to be a phylogenetic legacy retained from hermit crab ancestors whose coiled abdomens had evolved to fit nicely into deserted snail shells that hermits adopt as protective homes.) Which came first in evolution, the chicken or the egg? (The hard-shelled egg came first, by ≈300 million years.)

Assignment: Educate the Public to Nature's Marvels

> In the end, we conserve only what we love. We will love only what we understand. We will understand only what we are taught.
>
> Baba Dioum, Senegalese poet

A sad predicament for conservation efforts in the modern world is that a large fraction of humanity is estranged from nature, a situation that is likely to get worse as urbanization increases and human numbers soar. For example, I teach at a major university most of whose undergraduate students come from the metropolitan Los Angeles basin, and relatively few of those students seem to have had much opportunity for substantive personal contact with nature. Furthermore, our biology curriculum offers few "organismal" courses that might help to alleviate this problem. The situation here in Southern California is hardly unique. How can educators enthuse their students about biodiversity when direct experiences with nature have not been a significant part of those students' upbringing?

The good news is that many students (as well as many members of the general public) seem willing and eager to embrace nature if simply given the opportunity. Therein lies a third grand mission for molecular genetics and the other biodiversity sciences in conservation efforts: to cultivate in students of all ages a sense of awe, respect, and appreciation for the numerous other creatures—including the charismatically challenged—that share our crowded and imperiled planet. As phrased by E. O. Wilson (1984), "to the degree that we come to understand other organisms, we will place a greater value on them, and on ourselves." And, as noted by the late Stephen J. Gould (1991), "We cannot win this battle to save species and environments without forging an emotional bond between ourselves and nature . . . for we will not fight to save what we do not love."

An emotional and intellectual appreciation of nature, and also of rational scientific efforts to comprehend its workings, can be stimulated in many ways. Visual presentations (such as the *Life on Earth* TV series or the *March of the Penguins* movie) can play huge roles in educating the public. So too can eloquent thoughts and words, spoken or written. Fortunately, many biologists take delight in conveying the excitement of natural history and the joy of scientific inquiry to their students and also to the general public via trade books, lectures, service in conservation organizations, and other venues. Such efforts should be encouraged, applauded, and rewarded because only an educated public is motivated to demand a place for nature on this human-dominated planet.

CONCLUSION

The next few decades offer our best and last remaining chance to shepherd appreciable biodiversity through the current global extinction crisis. This monumentally important task should be at the forefront of societal consciousness and action not only because nature offers vast economic and material benefits to humanity, enriches our lives both aesthetically and intellectually, and provides bountiful scientific opportunities to understand the biological context of our existence. More basically, we should cherish nature because it is the ethically proper thing to do. Protecting what remains of nature must become our collective moral imperative. If it does not, we will lose not just nature herself, but also a deeply basic element of our humanity. We must come to value nature for nature's sake (as well as our own), instill that fundamental ethos in our children, and bequeath to future generations a planet that is no less biodiverse than the one into which we were born.

16

Engaging the Public in Biodiversity Issues

MICHAEL J. NOVACEK

To engage people in biodiversity and other environmental issues, one must provide the opportunity for enhanced understanding that empowers individuals to make choices and take action based on sound science and reliable recommendations. To this end, we must acknowledge some real challenges. Recent surveys show that, despite growing public concern, environmental issues still rank below many other problems, such as terrorism, health care, the economy, and (in the U.S.) family values. Moreover, much of the recent upswing in interest in the environment is due to the marked shift in attention to global warming away from other environmental problems such as destruction of ecosystems, water pollution, overpopulation, and biodiversity loss. Such a change in public focus often comes with a tendency to decouple various environmental problems and ignore their synergistic effects. Exacerbating this problem are arguments from the media and other sources that discourage public interest in environmental topics by characterizing the science behind them as overly complex, immersed in debate and controversy, and detached from human interests. Educational programming, media, exhibitions, and other means of public outreach should build on the welcome increase in public interest in global warming by demonstrating the interplay of various environmental disruptions. In the case of biodiversity, the importance of species in providing ecosystem

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American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024.

services, natural beauty and pleasure, and sustaining human lives is a message that requires constant attention and recrafting to impact diverse audiences.

The last decade of the 20th century was the first time a sense of urgency about the global-scale degradation of natural habitats, and the resultant threats to potentially millions of species, galvanized an effort to both study and conserve what was at risk. Edward O. Wilson (1988) was the first to publish the word "biodiversity" in the 1988 proceedings from a conference held in 1986 organized by W. J. Rosen, who originally coined the term. The current decimation of species, commonly called the biodiversity crisis, was the subject of Wilson's landmark book entitled *The Diversity of Life*, published in 1992. Subsequently, many other publications (Peters and Lovejoy, 1992; Heywood and Watson, 1995; Eldredge, 2000; Mooney and Hobbs, 2000; Novacek, 2001a, 2007; Wilson, 2002) have addressed this problem. By the late 1990s, biodiversity became the subject of elementary, secondary, and college courses, public journalism, television specials, and major museum exhibits. If biodiversity was still not a commonly recognized word, a broader public at least seemed to be getting the message that precious natural habitats and their species were under intense siege. In addition, scientific institutions, nongovernmental organizations (NGOs), and other groups pushed for more science and more effective policy to improve our stewardship of biodiversity under threat. Some governments reacted by adopting laws, regulations, and programs that limited overharvesting of both marine (Safina *et al.*, 2005; Stokstad, 2006) and terrestrial (Blanc *et al.*, 2003) species, controlled selected invasive species (Normile, 2004), and secured protection for selected natural habitats (Foley *et al.*, 2005; Revkin, 2008).

Given all this enlightenment, commitment, and effort, it is sobering to reflect, nearly 20 years later, on the continued deterioration of the situation. Despite impassioned pleas and elaborate strategies for conserving rain forests, the rate of loss has hardly abated. Brazil, which holds ≈62% of all Amazonian rain forest, lost on average ≈18,100 km^2/yr between 1988 and 2006 but registered a loss of 27,400 km^2/yr in 2004. Brazilian deforestation rates decreased by 2006 to ≈14,000 km^2/yr, but this trend could be temporary, because falling prices of soya and the increased strength of Brazilian currency and government intervention contributed to the decrease (Malhi *et al.*, 2008). Africa, with a significantly smaller amount of forest cover, lost an amount of forest comparable to that for South America for the same time period (Mygatt, 2006). Other regions of the world, notably Southeast Asia, are recording similarly serious losses (Sterling *et al.*, 2006; United Nations Food and Agriculture Organization, 2006). The situation for many freshwater habitats in both temperate and subtropical areas is, if anything, worse (Dudgeon *et al.*, 2005; International Union for the Conservation of Nature, 2007). Marine ecosystems have likewise suffered from devastating reductions in fisheries (Crutzen, 2002) and the degradation of >50% for most coral reef systems (Pandolfi *et al.*, 2005). At the same time, there is even less investment in study and conservation of marine habitats than in terrestrial ones (Hendriks *et al.*, 2007).

The obvious question, then, is why has a massive, international effort to deal with the biodiversity crisis failed to launch? Much of the current stasis is ascribed to the antagonism of corporate interests and lack of vision, and even resistance, of leaders and governments (Biodiversity Project, 2002; Shellenberger and Nordhaus, 2007). Accepting these as factors does not, however, obviate the need for broader and deeper public understanding. The "power of the people" is well demonstrated as the primary force behind new, more enlightened, measures by governments and corporations. Conversely, if a lack of public understanding or concern persists, it is highly unlikely that either governments or businesses will change course.

So, what can we now do to improve the situation? Scientists are obviously a critical part of any effort, because they continually improve the database for both species diversity and loss and thereby provide an ever clearer picture of the scientific realities of the biodiversity crisis. However, given the urgent and serious nature of biodiversity degradation, scientists also must have a voice in a dialogue that fosters broad public interest, commitment, and engagement. Here, I further probe the current state of public awareness of the biodiversity crisis, describe the challenges to achieving broad-based effective engagement on the issue, and offer further suggestions for dealing with these challenges.

STRATEGIES FOR ENGAGEMENT

To engage people in environmental issues such as the biodiversity crisis, one has to inspire a connection with nature. That linkage should be built from a clear and compelling message about the importance of biodiversity and what we risk in depleting it. However, these are only the first stages of a strategy that leads to engagement. As various dictionaries define the word, "engage" also means to develop meaningful connections with others; to bring into association or aid; or to attract, hold, or draw others into some agreed-upon action or service. It is clear that much of the effort to generate interest in environmental problems stops short of a follow-through that could be characterized as engagement. Surveys on "green" consumerism (Hartman Report, 1996) have shown that environmental awareness does not necessarily affect behavior and purchases.

Increased public interest in environmental issues (Biodiversity Project, 2002) by no means ensures that people will engage in ways that may modify their behaviors, adjust their priorities, and advocate the need for change.

The numerous impediments to achieving both public understanding and engagement on biodiversity issues, as related in the seminal 1998 Biodiversity Project "roadmap" report (Biodiversity Project, 1998), include science illiteracy, the related lack of public familiarity with ecological and evolutionary processes that inform conservation issues, an uncertainty as to why biodiversity conservation is good for individuals and society, a lack or impoverishment of experiences that put people into nature, the disinterest or even antagonism of media and other potential partners in outreach, mistrust of government, information overkill, and competitive choices (even often subliminal ones), such as unsustainable consumerism.

So, then, how shall we carry on with the mission? Recommendations, both specific and general (Biodiversity Project, 1998), include a clearer identification of the attitudes and understanding of diverse target audiences, greater investment on the part of scientists in public education and policy dialogue, notable improvements to science education, more strategic use of the media to reach the public, increased use of the Internet to reach new and expanded audiences, and more strategic ways of contacting and influencing policymakers and government and corporate leaders. These recommendations are embedded in the missions of numerous outreach programs, agencies, and nongovernmental organizations. Many of these recommendations are infrastructural, and they represent intensive long-term investments. This is commendable, but the approach may not develop at a rate fast enough for urgent response. For example, the poor state of science education in the U.S. and certain other countries (National Science Foundation, 2001) is an enormous problem that requires major correction. However, educational investments that might optimistically benefit emerging generations will not have an impact on people who have already experienced the system (Falk *et al.*, 2007). These are the adult populations who must engage now to deal with the crisis at hand. Mechanisms are required to deliver clear messages to very large and diverse audiences and elicit action over a short timescale.

In this chapter, I offer a few thematic recommendations, some of which blend with those already proposed, some of which add to them, and some of which reflect more recent shifts in public attitudes toward environmental topics, such as global warming. With this come suggestions for a few course corrections. The basic goal, namely to promote broader and deeper understanding and more committed stewardship of biodiversity, requires a multidimensional strategy, but one that focuses on three major objectives: (*i*) improved understanding of the diverse public audiences we are trying to reach, (*ii*) crafting of the messages suitable for those diverse audiences, and (*iii*) enhancements of the mechanisms for delivering those messages and eliciting engagement.

UNDERSTANDING THE AUDIENCES

Any strategy for engagement starts with the knowledge of who is being engaged and what they already know and do not know. Accurate information on the level of understanding of various target audiences is essential. Unfortunately, substantive research on the public understanding of biodiversity is still deficient, to a large extent because it has glossed over the relationship between people's understanding (as opposed to perception or opinion) and their decisions and actions (Bride, 2006). This is a serious gap in information, because studies expectedly show that acquired knowledge of a subject has a heavy influence on subsequent attitudes and behavior (Kaiser *et al.*, 1999; Bride, 2002; Kaiser and Fuhrer, 2003).

Some Public Misperceptions

That a deficit in knowledge leads to ambivalence or ill-advised conclusions and actions is clearly evident in the case of biodiversity conservation. An immediate obstacle, one noted from the outset (Biodiversity Project, 1998), is the use of the word biodiversity itself, hardly a word of common parlance. Surely biodiversity does not have the immediate recognition of phrases denoting other environmental aspirations, for example, "pure water" or "clean air." Even when one moves closer to its real meaning, the word biodiversity suggests only that there is a great variety of life forms; it does not lead one to recognize the interconnectedness of these forms in ecosystems. At the very least, the word requires vigilant and repeated explanation when communicating with the public, and this is a disadvantage in an age when metaphors and sound bites carry so much weight (Lakoff and Johnson, 1980; Lakoff, 2002).

Even if people have grasped the meaning of biodiversity, they are often unfamiliar with the meaning and significance of biodiversity loss. There is a persistent widespread misperception, for example, that what we are witnessing is merely the current wave of extinctions that are part of the normal turnover in the history of life (American Museum of Natural History, 1998). In other words, life on the planet has experienced myriad extinction events over billions of years, and it will continue to thrive, offering new opportunities for new better-adapted species. (Ironically, those who accept this pattern of life's constant turmoil often comfort themselves by exempting humans.) Indeed, the difference between mass extinction vs. background extinction rates is not one that has been readily absorbed by a large segment of the public (American Museum of Natural History, 1998). In addition, there is a tendency to place greater value on the more familiar and charismatic in nature rather than recognizing the integral roles and importance of all species, even insects, worms, fungi, and microbes, in various ecosystems (Wilson, 1992; Novacek, 2007).

Both of these misperceptions clearly impede the cultivation of a sense of concern and stewardship for the planet's eroding biodiversity. The notion that current rates of extinction are "normal" obviously prevents a focus on the urgency of the problem. Indeed, this perspective has fed an attitude, often expressed in the political arena, that action is unwarranted for something that, according to scientists, is no problem at all. A lack of appreciation for the richness and interconnectedness of diverse species, from elephants to soil bacteria, yields a distorted picture of what is really at risk. With such a narrow vision, even conservation efforts may place too much attention on a few endangered species rather than the ravaged habitats within which they live.

Evidence of Positive Public Response

However, there is also evidence the public is prepared and motivated to understand the biodiversity crisis more accurately and profoundly. Since the mid-1990s, several surveys have monitored public attitudes on biodiversity loss and biodiversity conservation. Prominent among these were the polls of Americans in 1996 and 2002 conducted by the Biodiversity Project (1996, 2002). Respondents in both polling years showed a high level of concern for the loss of species and degradation of environments. When they were given a definition for biodiversity, 47% of the respondents in 2002 (Biodiversity Project, 2002) and 41% in 1996 (Biodiversity Project, 1996) stated that stemming the loss of species was very important to them personally. In the 2002 poll, 69% stated they had a personal, and 65% said they had a moral, responsibility to protect all plant and animal life. Also, half (in 1996) or slightly more (in 2002) of the respondents strongly supported the Federal Endangered Species Act.

Another important aspect of public attitudes toward biodiversity is the high level of influence of aesthetic, ethical, patriotic, familial, and religious values in motivating a sense of responsibility for stewardship. In the 2002 Biodiversity Project poll, 64% regarded a wide variety of animals and plants as one of the most important things in their lives, and 71% felt that nature provided them with inspiration and a peace of mind. Respect for God's work, respect for nature for its own sake, the need to provide for future generations, the appreciation of the beauty of nature, the need to maintain a balanced healthy life, and the expectation as an American citizen to protect natural resources all were regarded as "extremely important" reasons for protecting the environment by a large percentage of respondents. These are important connections, because they pave the way to educating the public on biodiversity issues in ways to which they personally respond.

Shifts in Public Attitude: The Example of Global Warming

As noted, public awareness of the biodiversity crisis has risen slightly since the mid-1990s. However, this trend is now overshadowed by a greatly increased interest in global warming and climate change. The shift in public attention to this issue in the last few years is remarkable. In earlier polls (Biodiversity Project, 1996, 2002), people who "identified extremely serious [environmental] problems" ranked global climate change below virtually every other category, including land development, loss of rain forests, and damage to the oceans. More recent surveys, including notably the recently published Massachusetts Institute of Technology (MIT) poll (Curry *et al.*, 2007), show a radical reversal in public interest. Global warming now clearly occupies the top of the list of serious environmental problems faced by the U.S. by a wide margin, as judged by nearly 50% of respondents in 2006 as opposed to only 20% recorded by an MIT poll in 2003 (Curry, 2004). By contrast, primary concern over other environmental problems since 2003 either was virtually unchanged (destruction of ecosystems and overpopulation) or had markedly declined (water pollution, toxic wastes). It is noteworthy that endangered species ranked very low as a primary concern ≈5%) in the MIT polls for both 2003 and 2006. What accounts for this dramatic shift in public interest toward global warming? Answers could be potentially instructive in efforts to deliver a more multidimensional and realistic message, one where biodiversity loss still looms important in the public arena. Climate change, like biodiversity loss, has its scientifically complex and more subtle facets. Yet climate-change scientists have consistently related their conclusions to easily understood events, rising temperatures, storms, droughts, sea level rise, and other phenomena that people already accept as important and consequential. It "only" remained for scientists to demonstrate to people that the climate change necessary to increase these events and intensify their consequences was already happening. The scientific community worked doggedly to this end, translating and explaining the accumulating scientific discoveries in ways that effectively reached the public and the media (Intergovernmental Panel on Climate Change, 2007). The breakthrough that came with powerful messages by notable leaders like Al Gore (2006) built on this long-term cultivation of the scientific side of the story.

Such attention, of course, is warranted; global warming is an extremely serious and far-reaching environmental problem. Yet the swamp-out effect that the current focus on global warming is having on other environmental topics once again illustrates the problem of changes in public opinion that are not adequately informed. There is now a tendency in public dialogue to decouple various environmental problems and ignore their synergistic effects. Thus, people may find it hard to recognize that it is the "double whammy" of climate change in combination with fragmented degraded natural habitats, and not climate change alone, that is the real threat to many species and ecosystems, including human populations marginalized and displaced by those combined forces (Lovejoy and Hannah, 2005; Malhi *et al.*, 2008). The destructive impacts of other forces in addition to climate change must be brought back into the dialogue, because some of their deleterious impacts are already apparent, or will be so, on a timescale much shorter than the one we are calibrating for the effects of global warming (Myers and Knoll, 2001).

Public Priorities: Where Does Biodiversity Rank?

It would be unfortunate to dwell at length on the unbalanced public perception of various environmental issues without recognizing perhaps the most fundamental obstacle in communicating the urgency of these problems. We humans, of course, are confronted with many problems, environmental or otherwise, and without some sense of priorities, we would be totally overwhelmed by them. Recent surveys (Curry *et al.*, 2007) show that in the U.S., environmental issues, even with the added concern over global warming, still rank below terrorism, the Iraq war, health care, the economy, education, the quality of government leaders, Social Security, illegal immigrants, and family values. One may have scientific, political, and social views that lead them to disagree with the higher rankings of some of these topics, but it would be absurd to claim that terrorism and health care do not warrant our serious attention. Nonetheless, environmental issues should elicit greater concern, simply because they are so integral to many of the high-ranking problems on the public radar screen. Biodiversity provides enormous actual and potential benefits in the form of food, pharmaceuticals, and other resources and commodities. The degradation of habitats and biodiversity has huge implications for human health, economics, political instability, and even conflict. As discussed below, the key approach lies in better communicating an essential message: biodiversity is not really in direct competition with many issues that people regard as critical to their health, wealth, welfare, and sense of responsibility to family and future generations.

Assessing Diverse Audiences and Attitudes

Many of the above-noted surveys are useful in detecting some general signals of response from the public. However, these surveys also show diverse responses that relate to particular levels of education, economic background, cultural affiliations, and religious beliefs. Environmental educators argue that the true complexity of the audience has not been sufficiently sampled and analyzed (Bride, 2006). For example, we are just beginning to survey people in developing countries faced with difficult choices because of their very poor standard of living (Agrawal and Redford, 2006). Here, we can take a lesson from business marketing strategies, wherein target audiences are identified and parsed for different approaches. This underscores the need for more surveys that identify groups according to their onset knowledge, economic status, cultural identities, and motivations (Falk *et al.*, 2007). Of course, this targeted sampling should be accompanied by the kind of general assessments that identify some of the overarching concerns shared by many different audiences.

CRAFTING THE MESSAGE

A consistent result in surveys of public attitudes is that the basic message, that the biodiversity enormously important to the sustainability of the environment and the quality of our own lives is at serious risk, is not getting across to many of the target audiences. Moreover, the message carries some unfamiliar terminology, as noted above in the case of the word biodiversity itself, that requires constant attention and clarification. When people are given a definition of the word, they respond in ways compatible with efforts to protect biodiversity, expressing concerns over the destruction of habitats and the loss of species.

This leads directly to a consideration of those messages that have been more effective than others in reaching the public. Such an assessment is difficult; surveys, for the most part, have been aimed at eliciting the very general responses noted above. The limited insights gained from those responses, however, suggest that the most penetrating messages are those that clearly relate scientific insights concerning biodiversity and biodiversity loss to more general environmental problems and, in turn, to problems rooted in common experience: poor water quality, depletion of fisheries, zebra mussels and other invasive species, forest clearing, open-pit mining, urban sprawl, and many others. For example, the concept of shifting baselines in fisheries (Pauly, 1995) describes a tendency to assume that ocean life is abundant and ocean ecosystems are healthy, even though they have experienced steady, albeit slow, deterioration. Thus, putative "recovery" in the populations of some species by no means indicates the species has been fully restored to earlier historic levels. The concept has resonance, because not only is it scientifically instructive, but also it directly relates to the availability of a food resource vitally important to humans. Likewise, arguments that relate biodiversity to land use (Foley *et al.*, 2005) not only illuminate basic scientific principles concerning the necessary interaction of species in providing habitats rich in resources, they also provide useful options for agriculture that achieve a balance between providing productive cropland and sustaining biodiversity. Biodiversity science, collecting, surveying, identifying, classifying, mapping, and analyzing species, of course provides the important database for all these arguments (Wilson, 1992), but the public recognition of the importance of this work is elusive without themes that address more familiar issues.

Such themes then offer a chance to respond to the frequent question raised by people: Why should we care? The framework for the answer to this question was established some time ago by Ehrlich and Wilson (1991), namely, (*i*) we have, as Earth's dominant species, an ethical and moral responsibility to protect diverse life; (*ii*) biodiversity has conferred enormous economic benefits to humans in the form of foods, medicines, and industrial products; and (*iii*) species are the working parts of natural ecosystems that provide the essential services necessary to sustain life. We can use this framework to develop examples of messages that might more effectively intersect with current public attitudes.

The Ethical, Moral, and Aesthetic Argument

Because biodiversity is also synonymous with nature enriched, it appeals to what might be characterized as more noble human qualities; ethical and moral responsibilities; altruistic concern for our future generations and companion creatures; and aesthetic responses to the wonder, beauty, and tranquility of nature. As noted above, surveys show these motivations are strongly influential in raising public appreciation for biodiversity and concern for its erosion. Developing messages that draw on these instincts, what E. O. Wilson (1984) originally coined as "biophilia," the human need and love for nature, can only be advantageous. In museum exhibitions dealing with biodiversity, for example, the first step is often to place people in a stunning environment, one that reminds them of the beauty and wonder of nature, as a way of telling them what is at risk. A multipoint proclamation for a biodiversity agenda is not a way to greet visitors. A diorama of a rain forest or a wall displaying the extraordinary diversity of life forms is a more effective gateway. Some of the most effective television and film programs, such as the Discovery Channel 2007 series *Planet Earth* (Weprin, 2007), that speak to biodiversity themes use a similar approach in reinforcing the biophilia of viewers.

Many moral and aesthetic values that connect people with nature are inspired by people who, by relating their personal experiences, make a compelling case for stewardship. Humans are interested in other humans, not only what they do but also what passion drives them to do it (Fleischner, 1990). The roots of environmentalism are found in places like Walden Pond, where emotion, art, and experience play a critical role in defining the value of nature. Not everyone can write like Thoreau, but when a biologist effectively relates his or her personal and emotional, and intellectual, experiences in the field and the laboratory, people respond.

The Economic Argument

As Ehrlich and Wilson (1991) stated, biodiversity has unquestionable economic value in terms of foods, medicines, and other benefits. Nonetheless, elaboration of this point must be carefully crafted. The economic argument may encounter objections from people who fail to understand why it is more important to preserve habitats than to log, farm, or develop them for more immediate and competitive economic needs. Conflicts in economic perspectives are also now apparent even in different groups who identify themselves as environmentalists. Some favor accelerated economic growth as a way of producing the wealth, education, and technological breakthroughs necessary to solve the big environmental problems (Shellenberger and Nordhaus, 2007). However, there are those who advocate a massive return to local "green" economies, that depend critically on both individual and cooperative behaviors for moderation and the reduction of consumerism (McKibben, 2007). Connections must be made between the stewardship of biodiversity and different models for putatively compatible economies. We also need to understand much better the complex economic, traditional, cultural, and environmental interrelationships of low-income people in developing countries, many of whom live in the most biologically diverse regions (Agrawal and Redford, 2006). An effective argument here is that biodiversity emphatically plays a role in strategies for more sustainable agriculture, one that calls for the development of croplands that mix agriculture with natural components and thus provide both crop foods and restored ecosystem services (Foley *et al.*, 2005).

Another way of demonstrating the economic importance of biodiversity is to use examples of negative impacts of biodiversity loss. Such losses can destabilize relationships of communities, even countries. A perfect ecological, economic, and political storm is brewing in West Africa because of the complex interplay of overfishing by both African and European nations offshore, the accelerating devastation of wildlife on land for bushmeat, and periods of massive food shortages (Brashares *et al.*, 2004).

Human population densities in Africa are higher where biodiversity is higher, suggesting that biodiversity is itself a better index for comparative wealth than we once had realized (Balmford *et al.*, 2001). Biodiversity enrichment, in its transformed mode, means arable land, a great enticement for needy and opportunistic nations. Such pressures lead to conflict. Many important areas rich in biodiversity lie on international borders, especially tropical rain forests between nations that have not always maintained the most peaceful relations. History shows that people have made war over gold, oil, and water; they may do so over biodiversity.

The Ecological Argument

That species are the fabric of ecosystems, which in turn provide essential services, is a powerful concept, but one that may escape many of those unfamiliar with biological principles. Again, in many instances, it is best to enter these discussions from a practical and experiential starting point, often with a focus on current news. For example, animal pollination of plants is not only central to the function of terrestrial ecosystems, but it is also essential to the survival, sustainability, and economies of human populations (McGregor, 1976; Southwick and Southwick, 1992). The distressing recent decline in the health and number of managed bee colonies in the U.S. (Allen-Wardell *et al.*, 1998; Oldroyd, 2007) can be mitigated by greater reliance on wild populations of pollinators, so long as we maintain the natural habitats adjacent to agricultural areas that are necessary to support these wild species (Kremen *et al.*, 2002; Ricketts *et al.*, 2004). Thus, an effective public message is one demonstrating that putting more biodiversity into service can improve crop yield and save more than a little biodiversity-enriched land in the process.

This argument relates to one that inculcates a more general appreciation for the preservation of the natural world: pollination of plants by diverse species is not only important in food production of humans but is also critical to the sustainability of many terrestrial ecosystems. In other words, the world that is so familiar to us is strongly shaped by an extraordinary collaboration between flowering plants and pollinating insects (as well as some mammals and birds), a proof of concept with a 100 million-year-old history (Novacek, 2007). Huge losses of species that participate in this system have the potential to disrupt ecosystems in ways documented for plants and insects at the time of the end-Cretaceous extinction event (Wilf *et al.*, 2006). That history records such disruptions is a lesson of the past that people respond to; it induces them to think about what life might be like in a similarly degraded world of the future.

Relating Biodiversity to Other Environmental Issues

Explanations of the importance of biodiversity should also be contextual. How we deal with the synergy of destructive environmental forces will define our future. Importantly, the combined effects of climate change, fragmented and degraded habitats, and threats to biodiversity need a more compelling presentation to reach many audiences preoccupied with global warming as the one big environmental problem. Disturbing examples of synergistically driven devastation are all too common. The traumatic effects of both predicted climate change and the fragmentation of natural habitats may force near-term extinction of many species in the extraordinarily beautiful Fynbos flora of South Africa (Midgley and Miller, 2005). Overharvesting, pollution, ocean warming, and coral bleaching have irreparably damaged many of the world's coral reefs (Pandolfi *et al.*, 2005). Large-scale eutrophication in many coastal regions of the world has resulted in hazmat environments deadly to marine fish and plants and harmful to humans (Sellner *et al.*, 2003). In terms of solutions that address global warming, biodiversity-enriched forests are important in reducing our carbon footprint (Lovejoy and Hannah, 2005) or in mitigating the effects of urban heat islands (Foley *et al.*, 2005). Educational programming, media, exhibitions, and other means of public outreach should build on the welcome increase in public interest in global warming by demonstrating the synergistic effects of other environmental disruptions.

DELIVERING THE MESSAGE AND ELICITING ENGAGEMENT

The next step in the process of engaging the public, the delivery of the message, is perhaps the most challenging to the scientific community. This endeavor relies on such activities as market testing and targeting; media networking; exhibitry; filmmaking; legal, policy, and economic consulting; and organizational and collaborative programming that generally lie outside the expertise and experience of scientists most familiar with the problem. At an early stage in the biodiversity conservation effort, this challenge was recognized. Strategies were developed for convening, collaboration, and communication among professional groups, NGOs, media, and others. Subsequently, many NGOs (including those staffed with biodiversity experts) have been active. A comprehensive examination of these mechanisms and strategies for delivering the message lie beyond the scope of this chapter. Here, I focus on some practical issues that involve a few key elements in the process: the media, venues for public science education, and public participation, sometimes also referred to as "citizen science."

The Media as Audience and Partner

Effective linkages between the scientific and conservation community and the public must be made through the main channel of dissemination, namely media in the form of news and educational programming. Most adults learn about science through television, with print media running a distant second (National Science Board, 2004). Some biodiversity conservation strategies recommend that media be "used" to influence sectors of the public (Biodiversity Project, 1998). Initially, however, the news media should be recognized as another segment of the public audience, not as a partner. Journalists do not think of themselves as collaborators. Rather, they are tasked to observe and relate, although the expectation for even-handed treatment does not eradicate a slant in a story that arises from a particular point of view (Cunningham, 2003). Thus, media can be ambivalent, even antagonistic, to the idea that a particular scientific result and its implications are credible and important. News outlets are sensitive to popular tastes and, as such, rank the importance of many topics far higher than the loss of biodiversity (Biodiversity Project, 1998). Also, in many cases, media either tend to oversimplify scientific results and conclusions or overstate the lack of resolution on an issue, even when there is only a modicum of uncertainty to a result (Friedman *et al.*, 1999). One outcome is that news outlets can discourage public interest in environmental topics by characterizing the science behind them as overly complex, immersed in debate and controversy, and detached from human interests. Another reality of news coverage that frustrates an effort to cultivate public interest in an issue such as biodiversity loss is that stories die easily. The discovery of a hirsute deep-sea crab (Dean, 2006) or a new species of centipede in Central Park (Stewart, 2002) may make front-page and network prime-time news, but the resonance of the story is quickly lost.

Yet the capacity of the news media to respond to environmental issues and transmit them to a very broad and diverse public has been resoundingly demonstrated. Again, the example of the global-warming issue is relevant here, because it has somehow caught the current of a media deluge (Bowman, 2007) that has clearly had an impact on the public and ultimately on at least some of the legislators they vote for (Kintisch, 2006). Contributing factors here are doubtless persuasive and influential communicators like former Vice President and Nobel Laureate Al Gore (2006), new and cumulative scientific discoveries, and the continued reinforcement (sometimes fallaciously) with human experience, where every sign from nature—hurricanes, drought, melting ice, or disease outbreaks—is associated with global warming. Finally, practical and pressing issues, such as the rising price of oil and the need for energy options in everyday life, have been linked to the agenda for mitigating the effects of climate change (McKibben, 2007). Media (and public) attention to global warming is instructive and underlies some of points already made about connecting biodiversity issues with practical public concerns and needs.

At the same time, it is instructive to consider some of the downside to the media obsession with the global-warming issue. One, as noted above, is the obfuscation of the multidimensional environmental crisis, of which global warming is part but not all of the problem (Lovejoy and Hannah, 2005). Second, many news reports and media stories have both oversimplified and oversensationalized the global-warming scenario, a serious liability in light of the decreasing level of trust the public has in the media (Bowman, 2007). Finally, it is unclear to what extent the media is helping to explain options for action and the choices we may face to deal with global warming.

An important strategy for raising the newsworthiness of the biodiversity issue and helping to ensure its accurate portrayal is ultimately educational. This means providing opportunities for journalists and reporters to encounter more translated versions of scientific stories or to convene as groups or individuals with scientists over an extended period. Journalists often express a need to get a bigger picture, but this is impractical with a pressing deadline for a story on a new scientific discovery. News and views items in widely circulated scientific journals like *Nature* or *Science* are important links to other news agencies. At the next level, special sections like the *New York Times* "Tuesday Science Section" allow for the development of themes over several weeks or months. Scientific institutions devoted to public education can be effective cultivators and conveners in this way.

Educational programming can be powerfully transmitted by media, as indicated by the large audiences that view nature programs and other science series on television. Over the past 10 years, the number of programs on network and cable devoted to science has proliferated, but this is not necessarily accompanied by an increase in the average quality and effectiveness of these offerings (Dingwall and Aldridge, 2006). Some programming, notably certain nature shows, in its superficiality may fail to challenge nonscientific notions like Creationism and Intelligent Design and may even implicitly endorse them (Dingwall and Aldridge, 2006). However, selected programs, such as the 2007 Discovery Channel series *Planet Earth*, whose premier attracted >2 million viewers (Weprin, 2007), project both the beauty of nature and an artful message that encourages stewardship of nature, one fully compatible with the agenda for biodiversity conservation. Such programs need to be emulated for their high quality, and they should stimulate further collaborations between scientists and skilled producers and filmmakers.

The obvious shift in media and communications since the inception of the biodiversity agenda involves the use of the Internet. Indeed, the

Internet is redistributing news audiences in radical ways that are seriously threatening some traditional news organizations, particularly local newspapers (Patterson, 2007). Many web sites, including those offered by university programs, public science institutions, and conservation NGOs, provide effective status reports on species and habitats at risk and steps taken toward remediation. Web-based initiatives that network scientific research results and, at the same time, provide broad access, such as the *Encyclopedia of Life* (www.eol.org) (Wilson, 2003), could potentially engage very large new audiences outside the scientific community and allow them to contemplate the staggering richness, beauty, and importance of biodiversity.

Venues for Public Science

Even in countries where science literacy is much higher than in the U.S., there are limited opportunities for the lay public to stay abreast of the rapid rate of scientific discovery (Falk *et al.*, 2007). Aside from popular science books, periodicals, films, television specials, and web offerings, the responsibility for providing lifelong exposure to science falls to museums, botanical gardens, zoos, aquaria, science centers, and similar venues devoted to the public education of science. These institutions are thus critically important in educating people on biodiversity issues and other environmental problems. That such institutions can offer an encounter with nature that is both vivid and authentic defines their cultural impact (Novacek, 2001b). Many people, especially in urban areas, will rarely, if ever, see a relatively unspoiled tract of woodland in their region, let alone a tropical rain forest. For these individuals, an encounter with nature means a visit to a museum or the like. The enthusiastic response of visitors to this opportunity can be appreciated in terms of the huge audiences such institutions attract. Over 865 million people visited museums (including gardens, zoos, nature centers, science centers, and others) in 1999 in the U.S. alone (Lake Snell Perry and Associates, 2001).

One important strength of such institutions as venues for communicating science is the feeling of trust they invoke in the public. Surveys show that natural history and science museums have extremely high credibility ratings (Lake Snell Perry and Associates, 2001). However, there is also evidence that such institutions have not fully capitalized on their reputation. Exhibits and educational programs that not only dazzle but also address issues of substance, including the biodiversity crisis, have been slow in coming. Many permanent museum exhibits with environmental topics have not been revised since they first opened decades ago or are not complemented by new halls that address current themes (Novacek, 2001b). Aggravating this problem is the uneven commitment to scholarly activity in many such institutions (Novacek, 1991). A shift away from fundamental research in some institutions prevents them from taking on topics dealing with leading-edge science or major issues, topics where expertise is critical and in-house expertise particularly advantageous. Top-flight scientific research in an institution devoted to public education is not an oxymoron, especially where those researchers are strongly motivated and skilled communicators.

In more recent years, there are notable signs of improvement on this front. Exhibits dealing with current environmental issues, including biodiversity, have proliferated. The California Academy of Sciences will reopen in 2008 in an entirely new structure devoted to both exhibition and research and collections, one of the largest high-grade green buildings in the U.S. (Barinaga, 2004). New partnerships among institutions have allowed the sponsorship and nuanced development of timely exhibits on such themes as endangered species, climate change, evolution, and water that offer clear and consistent messages as they travel to various destinations and new audiences both in the U.S. and abroad. This momentum is encouraging, but at the same time, many of these public institutions are facing severe financial pressures (Dalton, 2007) and other forces that may move them to dilute both their scholarly and educational programs. Their support is paramount if we expect to elicit improved public understanding of important issues like biodiversity loss.

Public Participation: Citizen Science

A relatively new effort aimed at eliciting public engagement, dubbed citizen science, involves public–professional partnerships that allow people of all ages an opportunity to participate in real scientific research and to interact with scientists in the process (Cohen, 1997; Brossard *et al.*, 2005). Although the formulation of the idea has some novel aspects, it is rooted in the activities of amateur naturalists dating back in European culture to the 1700s (Sparks and Carey, 1995). The hope is that this kind of proactive participation not only will contribute new data on species and habitats but also will increase the participants' understanding of the process and results of the relevant science (Tuss, 1996; Brossard *et al.*, 2005). Such enlightenment, it is further hoped, will strengthen participants' connections with both science and the environment in ways that cultivate a sense of stewardship.

The citizen science approach seems well founded, but there are a few impediments. First, developing programs that foster citizen science requires intensive investment of time and energy on the part of the professional community, entailing often greater commitment than lectures, editorials, popular writing, and other efforts to communicate with the public.

As a result, the number of people that actually have the opportunity to become citizen scientists is limited. The problem seems surmountable as more efficient programs linking scientists with science educators are being developed (Johnson and McPhearson, 2006). A second problem resides in the poor understanding of the impacts of citizen science programs to date (Brossard *et al.*, 2005). Some of the few studies available show that, although participants improved their knowledge and familiarity with a particular scientific topic, they did not achieve a better understanding of the scientific process or change their attitudes toward science and environmental issues (Brossard *et al.*, 2005).

However, there are now many examples of citizen science programs in the biodiversity area that seem to have beneficial outcomes. The *Bioblitz* biodiversity surveys (Roach, 2003) carried out in New York's Central Park, Washington, DC, and many other sites yielded new scientific results that not only further enthused participants and galvanized their activities but also attracted media interest. It seems that programs in citizen science have much potential if they allow more people to participate, their impacts are more thoroughly analyzed, and participants are better familiarized with the environmental issues that relate to their contribution (Brossard *et al.*, 2005).

CONCLUSIONS

A very large and diverse public demonstrates a connection with nature and a sense of concern about environmental problems (Biodiversity Project, 2002). However, these attitudes often are not accompanied by real understanding of biodiversity or a sense of how to take more effective measures in protecting and sustaining natural habitats and species. Moreover, the public places much greater priority on other problems, such as terrorism, health, and the economy, than on biodiversity loss. People also often do not recognize the implications of biodiversity loss in exacerbating many problems more familiar and more important to them. Nonetheless, the capacity of the public (and the media) to respond in a more massive and emphatic way to some environmental issues, such as global warming (Bowman, 2007), points the way for greater connections with the public on biodiversity issues. Given the recent transformation of public response, it is more important than ever to show that environmental degradation represents a multidimensional problem in which biodiversity loss and other factors, in addition to climate change, have serious impacts. We are thus still challenged with the goal defined for the biodiversity agenda nearly 20 years ago. We must provide the enhanced understanding of biodiversity and its degradation in a way that empowers people to make choices and take action based on sound science and reliable recommendations. In the meantime, many avenues for attaining this goal—communications through media, environmental NGOs, contributions of public science institutions, and the development of citizen science programs—have been established. Investments in these actions must be strengthened and their strategies revisited and refined. Most importantly, the critical roles of species in providing ecosystem services, natural beauty and pleasure, and sustaining human lives bear a message that requires constant attention, recrafting, and improved deliverance to impact diverse public audiences.

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NOTE: A 2008 Gallup Poll shows that more Americans than ever recognize that the effects of global warming may have already begun but are not as concerned about this as they are other problems, including the pollution of drinking water (Newport, 2008).

17

Further Engaging the Public on Biodiversity Issues

PETER J. BRYANT

Scientists can do only a small fraction of the monitoring that is necessary to document changes in the populations and distributions of wild animals and plants, so the collection of such data often depends on organized efforts by members of the public with appropriate expertise. Regular butterfly, bird, and mammal counts as well as more comprehensive species inventories such as BioBlitz have been increasing in popularity and in reliability. The use of this kind of biodiversity data has been greatly facilitated by the ready availability of digital cameras and the huge opportunities for image sharing made possible by Internet access. Online communities of amateur naturalists are forming, and individuals are helping each other to find and to correctly identify wild species without collecting or destroying them. They are thereby contributing increasingly to our knowledge of the natural world and especially to changes brought about by human domination of the planet, including not only disappearances of native species, but invasion by exotic species and changes in distribution related to climate change. Unfortunately, these efforts are confirming that species of plants and animals are disappearing at rates that have alarmed even the most optimistic of scientists. Members of the public are also helping to monitor migration patterns; to rescue, rehabilitate, and release stranded, injured, or malnourished animals; and to restore damaged habitats including work to collect seed and propagate appropriate local varieties of plants. All of

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> these activities increase the level of awareness and thereby the level of concern felt by millions of citizens over human damage to the planet.

Scientists are finding extremely disturbing trends in many measures of the health of our environment, and they are continuing to document the ominous decline of many species and ecosystems. Some of the declines are enigmatic, some of them are beginning to be understood, and in some cases the causes are clear and are a result of human overexploitation, land conversion, or environmental contamination. Although it may be depressing to see so many signs of loss, it behooves us to document and analyze these changes so that we can start to understand the real costs of human domination of the planet.

Unfortunately scientists can do only a small fraction of the monitoring that these changes call for. Even if environmental science were well funded, we would still be faced with the problem that the data points (individual organisms or populations of animals, plants, or microbes) are often widely scattered over large areas, and data collection by remote sensing is now possible only for a limited set of the organisms of interest. The seasonality of distribution patterns is also of interest and compounds the problem of comprehensive data collection.

The public can be a tremendous resource for scientists interested in monitoring nature. There are plenty of skilled and observant people with knowledge of particular taxa or geographic areas, who are often passionate about these interests and are delighted to discover that their work may be useful. Many of them have independently developed knowledge bases and are collecting photographs of species, life cycles, behaviors, and the place of animals and plants in the wild. Others have become organized to carry out regular counts of birds or butterflies so that interesting trends may be detectable. Still more people have joined or started organizations for which one of the goals is to document and monitor certain taxa or geographic areas.

Although a global study of the engagement of the public in biodiversity issues would be of great interest, it has yet to be done, so some of my comments will be restricted to local trends in public engagement.

CALIFORNIA AND ORANGE COUNTY

Orange County is the smallest county in Southern California, with a total land area of 789 square miles, but its population of over 3 million people makes it the second most populous county in the state, with the highest population density (3,822 persons/square mile in 2004) outside of San Francisco County. Yet, as part of the California Floristic Province, one of the world's biodiversity hotspots, it retains an impressive flora and fauna. The southern part of the county still includes large, relatively undeveloped sections of coastal sage scrub habitat that have been recognized in the Orange County Natural Communities Conservation Planning (NCCP) process (Speegle, 2007).

Orange County contains significant populations of rare and endangered species of plants, birds, and mammals. It is home to over half of the remaining population of coastal cactus wrens (*Campylorhynchus brunneicapillus*; http://www.prbo.org/calpif/htmldocs/species/scrub/cactus_wren.html), and to over 15% of the remaining population of the California gnatcatcher (*Polioptila californica*; http://www.prbo.org/calpif/htmldocs/species/scrub/california_gnatcatcher.html), the country's largest contiguous population of this threatened species. In view of the huge rate of destruction of natural habitats in the county, we are probably losing countless species of less conspicuous animals and plants before they are even documented. Fortunately there is a remarkable level of public engagement on local biodiversity issues, and hopefully this engagement may help to prevent or slow the losses of biodiversity.

One of the most inspirational examples of local activity for biodiversity conservation is the work of Frank and Fran Robinson, who worked tirelessly from 1963 to 1973 to save Upper Newport Bay (http://www.newportbay.org/bayintro.htm) from development. The bay is now a 752-acre State Ecological Reserve associated with a 140-acre County Nature Preserve. It is home to thousands of resident and migratory birds as well as multiple other forms of marine and terrestrial wildlife. It will be mentioned several times in this chapter. Another hugely successful local effort, involving dedicated efforts by James Dilley, Elisabeth Brown, and others in the Laguna Greenbelt organization (http://www.lagunagreenbelt.org/History.html), led to the establishment of extensive protected areas in Laguna Canyon, now consolidated as the 6400-acre Laguna Coast Wilderness Park (http://www.lagunacanyon.org/index.html).

Identifying Species

Collecting data on any group of organisms requires, of course, accurate identification, ideally to species or even subspecies. Traditional field guides and web-based identification guides are becoming sophisticated and accessible, but most of us tend to develop expertise in a specific group of organisms. Sharing this expertise is a great way to engage the public in more data collection.

Arthropods (insects, spiders, crustaceans, millipedes, and centipedes) make up more than three-quarters of the species on Earth. However, the general public is not generally well informed about arthropods, and there are many misunderstandings and irrational fears regarding these animals. But as with most other animals and plants, to know them is to love them. A close look at a fly, a bug, or a roach can completely change one's feelings from aversion to fascination. With spiders, for some reason, aversions often run strong, but again a close look at the animal can often overcome these feelings.

A major factor in increased awareness and interest in arthropods has been the ready availability of digital cameras and especially the huge increase in opportunity for image sharing made possible by digital photography and Internet access. Web sites have facilitated image and knowledge sharing, and greatly stimulated efforts by amateur photographers to contribute to knowledge about biodiversity. Increased efforts to compile data on species distribution and migration are also adding to the popularity and utility of the combination of digital photography and web-based communication. New web-based interactive geo-informatics programs, such as Google Earth, provide exciting opportunities for cooperative data collection by scientists, and they also make it possible to involve the public in biodiversity data collection. This has the dual benefit of stimulating the public to understand the environment, and of producing important data that would be impossible to obtain by a typical scientific research group operating in isolation.

One of the more creative and successful uses of the Internet for engaging the public is the Bugguide web site, hosted by the Entomology Department at Iowa State University (Bartlett, 2007). In early 1999, Troy Bartlett of Roswell, GA, began sharing his insect photographs on the Internet. Noticing an unmet need, he decided to create an online community where both amateur and professional entomologists could not only view images, but also contribute their own images in order to get help with identification. The images are used to create guide pages that can subsequently be used to help others to learn and identify insects, spiders, and other related creatures in North America. Volunteer section editors contribute their expertise to review identifications and to move guide pages into the proper taxonomic positions. In many cases the photographs are good enough for identification to species, but there are still situations calling for microscopic examination of a specimen and even dissection of the genitalia by an expert. Images of such problematic creatures are still posted, but with more tentative identifications. Troy's Bugguide web site became such a success that Iowa State University was brought in to manage it. As of December 2007 it had 15,762 contributors, 75 editors, and 124,113 images on 8,624 species pages grouped into 667 families. It has also become much more than an identification guide, since it helps enthusiasts to compile and share information on life histories and geographic distribution of species.

It has the potential to make increasingly important contributions to our knowledge of biodiversity, to increase the sharing of this knowledge, and eventually to track long-term changes in biodiversity. The project could also be expanded to other taxa.

An alternative approach to engaging and educating the public about local biodiversity is to compile web sites showing only the species likely to be seen locally. By cutting down on the number of choices, this makes it much easier for amateurs to learn identification. With some other local photographers, Ron Hemberger, Hartmut Wisch, and I have compiled a web site on local (Orange County) arthropods that contains over 760 species pages and is one of the most complete displays of local arthropods to be found anywhere (Bryant, 2007a). I have also compiled a web site on the local intertidal animals, based on my own photographs and containing over 90 species pages (Bryant, 2007a). These projects have taught me and the other photographers a great deal about local biodiversity, and the web sites are used as field guides for untold numbers of the public who are curious or even worried about some of the creatures they encounter.

Orange County Birding (http://fog.ccsf.cc.ca.us/~jmorlan/ora.htm) provides a forum for reporting and discussing bird sightings in Orange County. Over 450 bird species have been recorded in the county. A special forum for reporting vagrants is the Orange County Rare Bird Alert (http://www.virtualbirder.com/vbirder/realbirds/rbas/CA.html#CAOC); 24 rare species were recorded during one of the most recent weeks.

Monitoring Populations

Some of the more conspicuous plants and animals are observed and counted annually by coordinated efforts across wide geographic areas. The July 4th butterfly counts in North America, organized by the North American Butterfly Association (http://www.naba.org/counts.html), are a good example. These are usually carried out by small teams of volunteers, each led by at least one expert in the local butterfly fauna. Each team designs a transect within a 15-mile diameter count circle and counts and identifies all butterflies observed from the transect, usually once per year on or about July 4th. In 2006, 483 counts were held in the U.S., Canada, and Mexico. The data are published annually and provide a wealth of information on population trends and geographical distribution of the species. Species diversity and abundance vary, of course, with location. The all-time record for most species on a California count was 78 species in Yreka, California, in 1991. Some species have population booms in some years and busts in others, making long-term trends difficult to document.

Our local counts (Upper Newport Bay, Orange County, California) have been taking place since 1987 and are unfortunately showing a disturbing decline in both numbers of individuals (4–500 in the late 1980s and early 1990s, but 1–300 since 1994) and number of species (over 20 in the late 1980s and early 1990s but 4 or less since 2004).

Butterfly counts in Northern California have also shown a serious decline. In 2006, Dr. Arthur Shapiro at UC Davis reported fewer butterflies in Northern California, particularly in the Central Valley, than at any time since he started counting them 35 years ago. At most of his study sites, he found only about half, or less than half, the number of species present in an average year. Near Vacaville in 2005, he found 378 individuals of 21 species, but in 2006 there were 43 individuals of 10 species (Kay, 2006).

Headlines like "Where have all the butterflies gone" are showing up in newspapers and journals in many other countries, including India (Khanna, 2005), Japan (Inoue, 2005), Canada (*Science Daily*, 2007), Australia (http://www.samuseum.sa.gov.au/butterflies/butterfly.htm), New Zealand (*New Zealand Herald*, 2007) and Britain (Butterfly Conservation, 2007a). The reasons for butterfly decline are usually not known, although pesticide use, genetically modified crops, climate change, habitat destruction, drought, and excessive collecting for trade are among the known causes or suspects.

In Britain, with a long tradition of public engagement in wildlife observation, over 10,000 volunteer recorders participate in assessing the distribution and abundance of butterflies over a network of over 750 geographic sites (http://www.butterfly-conservation.org/text/36/recording_monitoring.html), using a combination of weekly transect counts and single-visit timed counts. The comprehensive 2007 report (Fox *et al.*, 2007) shows that many of Britain's butterflies are, unfortunately, in a rapid and alarming decline. The Large Blue became extinct in 1979 and has been successfully reintroduced, but 76% of the 54 remaining resident species have declined. A related moth monitoring program including a National Moth Night assesses the distribution of moths throughout the country. Moths are much more diverse than butterflies, with about 2,500 species, and are not as well known but their numbers have also dropped, by about a third since 1968 (Butterfly Conservation, 2007b). Some moth species are seriously endangered and a few are thought to have gone extinct. British insect species that have disappeared in the past 50 years include 88 beetles, 56 butterflies and moths, 20 bees, 17 flies, 14 bugs and hoppers, and 12 wasps (McCarthy, 2006) making a total of over 200 extinctions. Three bird species and 20 plants have also been lost.

Sightings of butterflies by hundreds of volunteers are contributing to our understanding of climate change. This was seen most clearly in Britain, where April 2007 was the warmest April on record ending the hottest 12 months ever recorded. Associated with this climate change, 11 species of butterflies made their earliest recorded appearances and of 59 resident and regular migrant species, at least 36 emerged earlier than they would have done 10 years ago (McCarthy, 2007).

In the U.S., the Audubon Society's Christmas Bird Count is the world's longest-running uninterrupted bird census, engaging hundreds of volunteers every year. The complementary Breeding Bird Survey is a standardized count of birds along roadsides from May to July, carried out by volunteers and organized by the U.S. Geological Survey. Data from these two efforts were recently analyzed to discern 40-year population trends of all common North American bird species, and unfortunately the analysis revealed alarming declines of many of our most common birds. Some species declined by 80 percent, and 20 species lost at least half their populations over the study period.

For some declining bird species, some of the contributing factors can be identified. For example, meadowlarks favor farmland habitat, and this has been declining with changes in land use and the intensification of farming. Greater scaup and other tundra-breeding birds are suffering from loss of their permafrost breeding habitat and the arrival of predators from more temperate areas in association with global warming. Forest-dwelling birds, notably the boreal chickadee, are losing habitat due to various forms of deforestation.

Upper Newport Bay's Back Bay Science Center (Mallett, 2006) has developed a regular Marine Life Inventory program, carried out each month with the help of many volunteers. Otter trawls, plankton tows, beach seines, and mud grabs are used to collect both vertebrates and invertebrates from the bay, and the catches are brought ashore for species identification, measuring, and counting.

Captain Dave's Dolphin Safari (http://www.dolphinsafari.com/), based in Dana Point, Orange County, California, has been making use of volunteer dolphin and whale spotters on short cruises off the coast. During the 2007 season, large pods of bottlenose dolphins, common dolphins, Risso's dolphins, as well as surprisingly large numbers (up to 20 during a half-day trip) of blue whales were documented.

Monitoring Distributions

In addition to early appearances, several species are extending their distributions northward, according to data collected largely by volunteers. In Britain, the Essex skipper, the comma, brown argus, orange-tip, peacock, speckled wood, and ringlet are all expanding their ranges northward, consistent with the predicted responses to climate change (Briggs, 2006). In Orange County, California, the giant swallowtail first arrived in 1997 and has now been recorded from several cities in the county. The brown widow spider first appeared in 2005 and has been spreading to other cities

(Vincent, personal communication, 2007). One of our local insect photographers, Ron Hemberger, recently documented the first California record of a stripe-eyed hoverfly (*Eristalinus taeniops*), originally from Africa but previously recorded from Florida (Hemberger, 2006).

The new arrivals in Southern California also include well-documented pest species including Mediterranean fruit fly, Mexican fruit fly, oriental fruit fly, Japanese beetle, gypsy moth, ash whitefly, Eugenia psyllid, eucalyptus borer, Mexican scorpion, “killer bees,” and red imported fire ant, the latter being one of the “100 of the Worst” listed on the Global Invasive Species Database.

Black skimmers were seen at Upper Newport Bay first in 1987, then built up their population during successive seasons, reaching a total of over 500 in the late 1990s. They are now a regular and spectacular sight in the bay.

Another new arrival, first seen in coastal Orange County during the last five years, is the bobcat (Flynn, 2006). Its small population is being monitored extensively by the U.S. Geological Survey, using motion-sensing cameras, radiotelemetry, and recording GPS collars attached to the cats. But visual sightings and photographs from the public have also made an important contribution to our knowledge of the distribution and movements of these animals, especially in and near urban areas. These sightings and photographs are being used to monitor tagged animals, to match pelt patterns to identify individual bobcats, and the public has also been engaged in collecting information on road kills and their locations. This helps the professionals to learn more about the genetic structure of the bobcat populations and to start to better understand the impacts of habitat fragmentation and land-use changes on the populations. Knowing the locations of the road kills (16 in the San Joaquin Hills, Orange County, from September 2005 through April 2007) also helps to identify hotspots where animals are particularly vulnerable so that recommendations can be made for improved connectivity (Lyren *et al.*, 2006).

Monitoring Migration

Although designed primarily for K-12 students, *Journey North* (http://www.learner.org/jnorth/) is another Internet-based data collection project, focused on migratory species in North America. Students and the public participate in tracking the migration patterns of monarch butterflies, robins, hummingbirds, whooping cranes, gray whales, bald eagles, and birds and mammals. Sightings are automatically added to databases, which can be observed as animated maps on line. For whooping cranes, students can watch chicks grow and then learn migration as humans lead the way using ultra-light airplanes in *Operation Migration* (http://www.

operationmigration.org/). With bald eagles, students can collaborate with a biologist using satellite telemetry to track bald eagles to their nests in Canada. Regular reports are posted so that participants can see how their observations are used.

One of the best known and watched migratory species on *Journey North* is the monarch butterfly. However, both eastern and western populations of monarchs in North America appear to be in serious decline. For the eastern population, the number reaching their forested wintering grounds in Mexico in 2005 was the lowest since record keeping began about 30 years ago. For the western population, butterflies roosting at Pismo Beach, California, have had population fluctuations in the past, but there has been a steady decline from 115,000 in 1998–1999 to 22,000 in 2006–2007 (Barlow, 2008).

The annual migration of the California gray whale off the coast of California has been intensively monitored for 24 consecutive seasons by volunteers from the Los Angeles Chapter of the American Cetacean Society (Schulman-Janiger, 2007). Both southbound (December–February) and northbound (February–May) migrants are monitored from the Point Vicente Interpretive Center, 125 feet above sea level on the Palos Verdes Peninsula (Schulman-Janiger, 2007). In the 2006–2007 season, the census station operated for 166 days, averaging over 12 hours per day. Seventy-four volunteers contributed 7,697 effort hours on the program. Since many of the whales use offshore migratory routes, the counts cannot be used to determine the absolute population size, but they do provide useful data on seasonal use of the nearshore migratory path, reproductive rates, long-term population trends and behaviors including breaching, spyhopping, rolling, courtship, nursing, possible feeding, and interaction with other marine mammals and humans. The program also provides data on many other marine mammals that frequent the area.

Limits to Engagement

Although engaging the public in biodiversity is often essential to generating the political support needed for biodiversity conservation, some areas become so popular with the public that limits must be placed on visitation. National parks, of course, must limit visitation in order to preserve the resource and to maintain the quality of the experience for visitors. But similar problems exist outside the parks, as we have seen locally with tidepools, always a source of fascination for visitors but seriously limited in area and highly vulnerable to damage by collecting and trampling. This problem has been addressed in a new and quantitative way by the Tidepool Education Interpretive Program at the Treasure Island Seashore in Laguna Beach (Rosaler, 2007). Over a one-year period, 29,363 visitors were observed and 18,268 were approached by program staff for an "educational interaction." During that time the staff witnessed 1,205 infractions of the city's posted tidepool rules (Never pick up or remove animals, shells, or rocks; Do not pull animals off the rocks, or poke them with sticks; Walk gently, taking care not to step on plants or animals; Never turn over rocks). The study showed a low number (0–20) of infractions up to a certain level of visitation, but after the visitations exceeded about 250 people per day the number of infractions increased substantially. This suggested that at this population density the visitors become increasingly difficult to manage and that this particular beach had a visitor "carrying capacity" of about 250 per day, above which additional management techniques are required to prevent degradation of the resource.

Rescue and Restoration

The public is also engaged in biodiversity issues through animal rescue and habitat restoration programs. One of the most active animal rescue operations locally is the Pacific Marine Mammal Center in Laguna Beach (http://www.pacificmmc.org/), which was set up by Friends of the Sea Lion in 1971. Every year the staff and volunteers rescue between 150 and 200 marine mammals including California sea lions, harbor seals, and elephant seals and treat them for malnourishment, injuries, entanglement in fishing gear, and shellfish poisoning. Volunteers commit a total of over 25,000 hours per year to the program. The Wetlands and Wildlife Care Center in Huntington Beach (http://wwccoc.org/) also provides care and rehabilitation of native wildlife, with a capacity of 400 birds and mammals.

Many habitat areas in Orange County have suffered from years of overgrazing, spreading of invasive plants, and other forms of damage, and these areas are now being restored in volunteer efforts by many different organizations. These include ROOTS: A Community-Based Restoration and Education Program for Upper Newport Bay sponsored by the California Coastal Commission (Yurko, 2007). Volunteer duties include plant installation, invasive plant removal, site maintenance, site monitoring, native seed collection and propagation, administration, and educational efforts including school field trips and teacher workshops. Since 2002, 8,300 volunteers have participated, totaling 23,500 volunteer hours, and there are nine current restoration sites covering approximately 12 acres. A similar effort is Second Sundays (Naegele, 2007), managed by Orange County Parks, involving County staff and volunteers on over 5 acres of land, involving 2,200 volunteer hours during the first 7 months of 2007. A local nonprofit organization, Back to Natives (http://www.backtonatives.org/), also manages volunteer restoration programs. The Orange County

Parks Adopt-A-Park Volunteer Program works to maintain and interpret over 39,000 acres of parkland and open space throughout the county in collaboration with several nonprofit support groups. Their volunteer opportunities are listed on the Orange County Wild web site (http://www.ocwild.org/Files/volFlyerOC.pdf).

Some of our local restoration efforts have been managed for the benefit of individual endangered species. These include the Endangered Species Habitat Restoration Day at the Seal Beach National Wildlife Refuge, for the benefit of Belding's Savannah sparrow and the California least tern and organized by the Aquarium of the Pacific (http://www.aquariumofpacific.org/). A habitat restoration program by the Beach Bluffs Restoration Project in Redondo Beach, California, was successful beyond expectations in bringing back the endangered El Segundo blue butterfly to its native habitat from which it had been missing for decades (*USA Today*, 2007).

Organizations Engaging the Public

Orange County is home to an amazing number of organizations and chapters of national organizations concerned with conservation of groups of animals or plants, or preservation of individual natural areas. They are too numerous to list here, but can be found on the Orange County Directory and Search Engine @OC (http://www.at-oc.com/community/environment.htm).

18

Where Does Biodiversity Go from Here? A Grim Business-as-Usual Forecast and a Hopeful Portfolio of Partial Solutions

PAUL R. EHRLICH and ROBERT M. PRINGLE

The threats to the future of biodiversity are many and well known. They include habitat conversion, environmental toxification, climate change, and direct exploitation of wildlife, among others. Moreover, the projected addition of 2.6 billion people by mid-century will almost certainly have a greater environmental impact than that of the last 2.6 billion. Collectively, these trends portend a grim future for biodiversity under a business-as-usual scenario. These threats and their interactions are formidable, but we review seven strategies that, if implemented soundly and scaled up dramatically, would preserve a substantial portion of global biodiversity. These are actions to stabilize the human population and reduce its material consumption, the deployment of endowment funds and other strategies to ensure the efficacy and permanence of conservation areas, steps to make human-dominated landscapes hospitable to biodiversity, measures to account for the economic costs of habitat degradation, the ecological reclamation of degraded lands and repatriation of extirpated species, the education and empowerment of people in the rural tropics, and the fundamental transformation of human attitudes about nature. Like the carbon "stabilization wedges" outlined by Pacala and Socolow (2004), the science and technologies needed to effect this vision already exist. The remaining challenges are largely social, political, and economic. Although academic conservation biology still has an important role to play in developing technical

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tools and knowledge, success at this juncture hinges more on a massive mobilization of effort to do things that have traditionally been outside the scope of the discipline.

The fate of biological diversity for the next 10 million years will almost certainly be determined during the next 50–100 years by the activities of a single species. That species, *Homo sapiens*, is ≈200,000 years old. It has been fabulously successful by ecological standards: it boasts as-yet-unchecked population growth and a cosmopolitan distribution, and it has vanquished its predators, competitors, and some of its parasites. The fossil record suggests that the typical mammal species persists for approximately one million years (Martin, 1993), which puts *Homo sapiens* in mid-adolescence. This is a fitting coincidence, because *Homo sapiens* is now behaving in ways reminiscent of a spoiled teenager. Narcissistic and presupposing our own immortality, we mistreat the ecosystems that produced us and support us, mindless of the consequences.

The state of biodiversity today is a reflection of that abuse, but the reflection is hazy because we know neither the total number of populations or species nor how many have gone extinct. Our best information is on the rate and extent of habitat destruction and degradation. For example, we know from long-term monitoring that coral cover in Jamaican reef ecosystems declined from >50% to <5% between the late 1970s and 1994 (Hughes, 1994). From remote-sensing studies, we know that the rate of selective logging in the Brazilian Amazon ranged from 12,000 to 20,000 km^2/year between 1999 and 2002 (Asner *et al.*, 2005) and that the rate of deforestation in the Peruvian Amazon averaged 645 km^2/year from 1999 to 2005 (Oliveira *et al.*, 2007). Likewise, we know from global mapping studies that nearly 50% of all temperate grasslands, tropical dry forests, and temperate broadleaf forests have been converted to human-dominated uses worldwide, whereas only 4–10% of those biome types are formally protected (Hoekstra *et al.*, 2005).

Of the total number of species on Earth, we still cannot say much more than that it is likely to be "of the general order of 10^7" (May, 1988). Estimates of species extinction rates—often based on estimates of habitat loss in conjunction with the species–area relationship—are similarly imprecise (May *et al.*, 1995; Balmford *et al.*, 2003b) and are sensitive to multiple assumptions [e.g., Regan *et al.* (2001) and Seabloom *et al.* (2002)]. The number of animal and plant extinctions certified since 1600 is only slightly greater than 1,000 (May *et al.*, 1995), but our pitiful knowledge of biodiversity's extent and the inherently inconspicuous nature of extinction ensures that this figure is a small fraction of the true number. Although no scientific consensus is forthcoming on the exact rate of extinction for any region or group of organisms, much less for global biodiversity, there is a consensus that current extinction rates vastly exceed background ones, perhaps by two to three orders of magnitude (Pimm *et al.*, 1995; Woodruff, 2001).

Although species loss occupies an overwhelming proportion of the literature, genetically distinct populations are also an important component of biodiversity. Estimates of population diversity and extinction rates are even more uncertain than those for species, but even these crude estimates are alarming: of perhaps 1 to 7 billion populations worldwide, 16 million may be extinguished each year in tropical forests alone (Hughes *et al.*, 1997). Trends in key parameters of well-studied populations are consistent with this picture of decline. Amphibian populations have declined locally and globally in recent years (Houlahan *et al.*, 2000; Rachowicz *et al.*, 2006), and many mammal species worldwide exhibit range-size contractions indicative of heavy population loss (Ceballos and Ehrlich, 2002).

When we were first asked to prepare a paper addressing the question "Where does biodiversity go from here?" a variety of cynical answers leapt to mind. The principal threats to biodiversity—direct overexploitation of organisms, habitat destruction and degradation, environmental toxification, climate change, and biological invasions, among others—have been known for decades. Yet despite a ballooning number of publications about biodiversity and its plight, there has been dispiritingly little progress in stanching the losses—so little that some commentators have characterized applied ecology as "an evermore sophisticated refinement of the obituary of nature" (Jackson, 2007). As conservation-oriented scientists, we are responsible for biodiversity. Its loss is our failure.

We draw on the literature to sketch a brief and incomplete answer to the question posed to us, assuming that society continues business as usual. Because that outlook is bleaker than we are willing to accept, we then outline a more hopeful set of answers. These amount to a portfolio of strategies for combating biodiversity loss.

BUSINESS AS USUAL: WHERE DOES BIODIVERSITY GO FROM HERE?

There are ≈6.7 billion people in the world as we write this, a number that is projected to grow (according to a mid-range forecast) to 9.3 billion by 2050 (Population Reference Bureau, 2007). The continued growth of the human population displaces biodiversity directly, as land is developed to create living room. In one recent example, Venezuelan president Hugo Chavez aims to translocate 100,000 people into a brand new city in El Avila National Park to alleviate overcrowding in Caracas (Forero, 2007). Providing a huge global populace with the resources necessary for survival (much less comfort) also displaces biodiversity. A recent spatially explicit analysis showed that humanity already appropriates nearly a quarter of global terrestrial net primary productivity, and up to 80% in large regional swaths (Haberl *et al.*, 2007).

Supplying the consumption of the next 2.6 billion people will almost certainly have a greater environmental impact than supplying the last 2.6 billion added since 1975. Our species has already plucked the lowest-hanging resources and converted the richest lands. To maintain the pace, metals will have to be won from ever-poorer ores, and oil, natural gas, and water will need to be obtained from ever-deeper wells and transported farther—all requiring accelerating energy use. So-called "marginal lands," often the last holdouts of biodiversity, are the final frontier, awaiting conversion into more human biomass. Whenever biodiversity preservation poses a threat to human livelihood, comfort, or convenience, the politically expedient choice is usually to liquidate the natural capital. In sum, every increment in the human population accelerates competition with other organisms for Earth's primary production. And, of course, not only do the present poor need more consumption, the present rich also demand it—as certainly will the newcomers. This is all in the face of signs that average per capita consumption is already unsustainable in developed regions (Ehrlich and Goulder, 2007), indicating a stark tradeoff between today's consumption and the basic human rights of future generations.

A major byproduct of human consumption is the toxification of Earth's ecosystems. Human agriculture and fossil-fuel combustion have multiplied the emission and deposition of nitrogen in recent decades, with negative consequences for biodiversity in grasslands (Stevens *et al.*, 2004) and aquatic ecosystems (Carpenter *et al.*, 1998). Widely used herbicides such as atrazine and glyphosphate harm amphibians (Hayes *et al.*, 2002; Relyea, 2005), potentially contributing to global amphibian decline, and the use of antiinflammatory drugs such as diclofenac and ibuprofen to treat livestock in India has ravaged scavenging birds, for which cattle carcasses are a major food source (Oaks *et al.*, 2004; Cuthbert *et al.*, 2007).

Anthropogenic climate change stems from a special case of toxification: carbon pollution. Many biological impacts of global heating are evident, as animals and plants undergo changes in phenology, distribution, and local abundance (Parmesan, 2006). More alarming, anthropogenic heating has already been directly implicated in several extinctions (Pounds *et al.*, 2006) and seems likely to precipitate others. In the oceans, heating is already reducing the extent and altering the structure of coral reefs via breakdown of the coral–algal symbiosis (Hughes *et al.*, 2003). Moreover, rising CO_2 concentrations are lowering oceanic pH, with potentially disastrous consequences for coral reefs and other marine ecosystems (Orr *et al.*, 2005; Hoegh-Guldberg *et al.*, 2007).

Direct exploitation of wildlife species by human beings takes a variety of forms, from subsistence hunting (Brashares *et al.*, 2004) to the harvesting of wild plants and animals for conversion into luxury goods and pets (Root *et al.*, 2006; O'Brien *et al.*, 2003). Large mammals and fish suffer disproportionately from direct human predation. Many of these vertebrates (e.g., apex carnivores, large ungulates, etc.) are strongly interacting species in their native ecosystems (Terborgh *et al.*, 2001; Pringle *et al.*, 2007; Ripple and Beschta, 2007a; Palmer *et al.*, 2008), and overharvesting them may have destabilizing effects on biodiversity and ecological processes such as seed dispersal, nutrient cycling, and even primary production. In oceans, top piscivores suffer disproportionately as fleets fish down the food web (Pauly *et al.*, 1998). Industrialized fisheries have often devastated community biomass of predatory fish within a few decades (Myers and Worm, 2003), with even sharper declines common among the apex predators (Baum and Myers, 2004).

Nonnative species introduced by people into naive ecosystems have occasionally wrought havoc on local biodiversity via predation, competition, and the disruption of co-evolved interactions. Biotic interchange is likely to increase with increasing mobility in an increasingly globalized world; under business as usual, biogeography will be increasingly homogeneous.

A cryptic yet critical threat to biodiversity is the loss of future evolutionary potential. Extinction of genetically distinct populations, decreases in effective population sizes, and homogenization of habitat types are all likely to have negative effects on future biodiversity (Myers and Knoll, 2001; Woodruff, 2001). The positive relationship between speciation rate and habitat area (Losos and Schluter, 2000) indicates that decreases in species geographic ranges will diminish future speciation rates, which in turn will impoverish future diversity (Rosenzweig, 2001). Speciation of large vertebrates, which are highly mobile and require large habitats, may cease entirely (Woodruff, 2001), and biodisparity—the range of morphological and physiological variety on Earth—will decrease as phylogenetically distinct, species-poor branches are pruned from the tree of life (Jablonski, 1995).

Loss of microevolutionary potential will also limit the capacity of populations to adapt to changing environmental conditions, highlighting another important point: The drivers of biodiversity loss will often act synergistically in imperiling populations and species. Habitat loss and fragmentation compound the effects of climate change, as species are unable to track their thermal niches spatially (Travis, 2003). The interactions among logging, fire, and climate change threaten to transform the Amazon rainforest into savanna (Oyama and Nobre, 2003; Terborgh, 2007). Such positive feedbacks seem to be a rule, rather than an exception, and they make it impossible to generate precise estimates of future biodiversity.

In short, although there are many uncertainties about the trajectories of individual populations and species, we know where biodiversity will go from here in the absence of a rapid, transformative intervention: up in smoke; toward the poles and under water; into crops and livestock; onto the table and into yet more human biomass; into fuel tanks; into furniture, pet stores, and home remedies for impotence; out of the way of more cities and suburbs; into distant memory and history books. As biodiversity recedes, we also lose the stories that go with it and many ways of relating to the world in which we evolved.

We now consider what might happen if humanity changes the way it does business. Ours is not a comprehensive treatment of this issue. The Millennium Ecosystem Assessment (2005a) contains a thorough and colorful summary of the state of biodiversity, and it provides important (and necessarily overarching) recommendations for softening human impact on ecosystems—things like increasing governmental accountability, eliminating environmentally malign subsidies, and reducing greenhouse-gas emissions. However, the breadth and complexity of these objectives, and the considerable political clout required to enact them, can engender the misconception that only governments can determine where biodiversity goes from here. That misconception, in turn, is a recipe for paralysis among concerned individuals. Therefore, we try to focus more narrowly on seven more-or-less concrete sets of actions that individuals or small groups have already set in motion. If implemented more broadly and scaled up dramatically, these actions would collectively enable a different, more appealing fate for biodiversity.

Although each of the following strategies is being used somewhere, none is yet realizing its full potential. Some may not be achievable in all times and places, but none is exclusive of any other. Most of these strategies are familiar to most people in the conservation community; the notion that they are all "correct" ways to conserve biodiversity is perhaps less so. Indeed, squabbles over strategy are endemic within the conservation community, perhaps because different strategies are seen as competing for funding and for primacy in the scholarly idea-scape. The alacrity with which international conservation nongovernmental organizations have "branded" themselves (Rodriguez *et al.*, 2007) and the sometimes absurdly acrimonious exchanges between conservation academics seem to manifest a widespread "either–or" belief that there are absolutely right and wrong ways to protect biodiversity (Wiens, 2007b). Ostrom *et al.* (2007), in a recent *PNAS* Special Feature, wrote of the need "to go beyond relying on abstract cure-all proposals for solving complex problems related to achieving sustainable social–ecological systems." By emphasizing a portfolio of partial solutions, we hope to reinforce the idea that maximizing future biodiversity will require a plurality of approaches in creative admixtures that are tailored to local realities. Each place needs a different mixture.

BUSINESS AS UNUSUAL: WHERE ELSE MIGHT BIODIVERSITY GO FROM HERE?

Into a Less Peopled, Less Hostile Planet

The human impact on biodiversity is a product of three root factors, summarized in the heuristic I=PAT identity (Ehrlich and Holdren, 1971). The overall Impact (encompassing all of the drivers of biodiversity loss discussed above) is the product of Population size, per capita Affluence, and the Technologies (and socioeconomic–political systems) used to generate affluence. "Affluence" in this context is simply per capita consumption, and "socioeconomic–political systems" refer to the strictures that regulate technology use.

Tangible steps to reduce any of these factors will lessen their product and help produce a more hospitable future for biodiversity. A current example that integrates all three factors is the drive to produce biofuel (T) to satisfy the expanding energy consumption (A) of a growing population (P). Unchecked biofuel production has the potential to destroy all moist-tropical biodiversity that lacks conservation status. Biologically impoverished monocultures of oil palm, soybeans, and sugarcane for biodiesel and ethanol are devouring swaths of Brazilian Amazon and Cerrado, Indonesian, and Malaysian tropical rainforests and other vast reservoirs of biodiversity (Fearnside, 2001; Klink and Machado, 2005). However, the production of biofuels from native grassland perennials on agriculturally degraded lands has the potential to reduce carbon emissions without displacing food production or converting native habitats (Tilman *et al.*, 2006). In this case, an innovative Technological adjustment would reduce overall Impact. Likewise, simple shifts in socioeconomic–political systems—instituting high-occupancy vehicle lanes to reduce carbon emissions, for example, or demanding high-seas ballast water exchange for cargo ships to reduce species introductions—would do a great deal.

Although population growth has slowed or is slowing in many developed countries, it remains high in many developing regions. Much is known about how to hasten the transition to a stable and then declining world population. Education and employment—for women especially—along with access to contraception and safe abortions are the most important components (Rindfuss *et al.*, 1980). Less is known about how to prevent overconsumption of natural resources (Ehrlich and Goulder, 2007). Mass media are a powerful tool for raising environmental awareness and influencing attitudes toward consumption, as demonstrated by Al Gore and his documentary film *An Inconvenient Truth*. To this end, we should exploit the media to the fullest possible extent. Although more environmentally benign technologies will also help, the battle will not be won without a transformative collective decision by consumers that less can be more. For example, although an 80% shift from beef and pork to farmed fish and poultry could enable displacement of up to 22% of U.S. gasoline consumption with low-impact, high-diversity biofuel (D. Tilman, personal communication), such a shift will not happen without hundreds of millions of conscious decisions that a sustainable economy is worth more than the taste of bacon cheeseburgers.

Into Perpetuity via Endowments for Conserved Areas

As many conservation biologists have noted, formally protected areas are not realizing their full potential, being too few, too small, too far apart, too expensive to establish and maintain, and/or too poorly administered (Noss and Cooperrider, 1994; Kareiva, 2006). These pitfalls notwithstanding, nature parks and other conservation areas are central to the future of biodiversity (Terborgh and van Schaik, 2002).

The outstanding national parks of North America and Australia demonstrate that well-fed voter/taxpayers, whatever their environmental shortcomings, are at least willing and able to support biological preserves; people in poorer countries, the argument goes, cannot necessarily afford that luxury. Of the various forms of revenue used to support protected areas in poor countries, conservation trust funds—specifically, endowment funds intended to last in perpetuity—are the most promising. Unlike taxes, user fees, and debt swaps, endowments provide sustained funding and are relatively resilient to political whims and fluctuations in the demand for ecotourism (Spergel, 2002). As of 2000, conservation trust funds had been established in more than 40 countries, and nine developing nations boasted endowments of US$10 million or more (Spergel, 2002).

Spergel (2002) argues that conservation trust funds should be additional to existing government funding, but this may not always be the case. Consider the following initiative being considered in Costa Rica. It is called Paz Con la Naturaleza—Peace with Nature—and it aims, among other things, to generate $500 million to endow the country's entire conserved-area system. Crucially, this would relieve Costa Rican taxpayers of the burden of financing conservation. Under the plan, $100 million would be spent to consolidate the existing national park system—25% of the country—into 11 large conservation areas (Dalton, 2006; D. H. Janzen, personal communication). The remaining $400 million would be invested outside the country in a university-like endowment; $20 million of annual revenue from that endowment would be divided among the conservation areas and used to cover operating costs, with any remaining income plowed back into the fund for growth. Although the financing would operate at a national and international scale, the plan calls for decentralized local administration of the individual conservation areas. This plan, with an endowment as its centerpiece, simultaneously redresses most of the frequently cited shortcomings of conservation areas: it aims to make them bigger, closer together, better administered, and essentially free to their users (aside from the opportunity cost of the land use).

It is an ambitious goal, to be sure. The price tag is steep by traditional conservation standards, but with many U.S. research universities boasting endowments in the multiple billions of dollars, $500 million to conserve 25% of a nation and 4% of global biodiversity forever—creating the world's first explicitly green country in the process—seems like a bargain. It remains to be seen whether the plan can be implemented in small, stable, "green" Costa Rica, much less anywhere else; we will not know until money is pledged. In any event, perpetual endowment funds have tremendous potential in conservation [e.g., as a source of revenue for restoration and other projects; Spergel (2002) and Schuyt (2005)] and will generally increase the "localization" and longevity of conservation initiatives by tying funds to long-term programs in particular areas.

Into Human-Modified Landscapes, as Best It Can

Unbroken tracts of conserved wild area, if they exist, will always be the greatest reservoirs of biodiversity and the most interesting places to visit. But under certain conditions, human-dominated pastoral and agricultural landscapes can also harbor an appreciable amount of biodiversity (Western, 1989; Pimentel *et al.*, 1992; Daily *et al.*, 2001). Simple and inexpensive management techniques, such as maintaining living hedges around agricultural plots (Robinson and Sutherland, 2002) and preserving remnant trees in pasture (Luck and Daily, 2003), can often buttress the biodiversity of these areas.

There are many compelling reasons to conserve countryside biodiversity. One is that most human-dominated landscapes will not revert to wildness anytime soon; enabling wild populations to persist in these areas is the best plausible outcome for biodiversity. Another is that habitat types vary in their tolerance of human activity. Whereas tropical forests are quite sensitive to burning, wood chopping, and hunting, tropical savannas are relatively resilient to anthropogenic disturbance. In many parts of Africa, much or most wildlife occurs outside of nationally protected areas (Western, 1989), and wildlife can coexist alongside limited livestock populations (Georgiadis et al., 2007). That people also share this space does not necessarily diminish its conservation value. Moreover, maintaining nonconserved areas in biodiversity-friendly ways aids migration and dispersal between protected areas, a process that will become even more important as climate change rearranges species' distributions (Ricketts, 2001; Travis, 2003). Finally, maximizing biodiversity in areas where humans are active in their daily lives increases the frequency of interactions between human and nonhuman organisms, which enhances the potential for ecosystem-service delivery and bioliteracy development (see *Onto the Cultural Radar Screen*). Economic incentives (or legal strictures) can be developed to encourage (or require) biodiversity-friendly use of privately held lands (Farrier, 1995; Stoneham *et al.*, 2003).

Biodiversity maximization in human-dominated landscapes does not in any respect reduce the need for large conserved wildlands. How to allocate conservation resources among these two different frameworks is a local problem, and answers will vary depending on such factors as the habitat types involved, local land-use history, the state of the region's government and protected-area system, and the availability and price of land for purchase. As in most other respects, Britain is different from Kenya is different from Amazonia. The challenges in planning for conservation in human-dominated landscapes are perhaps most pronounced in fragmented tropical forest–pasture–field mosaics, because tropical-forest biodiversity is so great and the alternate landscape states are so dramatically different from the baseline. One uncertainty is whether the apparently high conservation value of these mosaics [e.g., Daily *et al.* (2001) and Mayfield and Daily (2005)] will be sustained over centuries, or whether it will ultimately succumb to the "extinction debt" (Janzen, 1986; Tilman *et al.*, 1994). A related concern is that the diversity of interspecific interactions in human-dominated landscapes will decline more quickly and less perceptibly than the diversity of populations or species and that this will eventually lead to additional population and species loss. A 300-year-old canopy tree species in a Brazilian pasture may serve as a roost for a diversity of birds, epiphytes, and other organisms. But if its pollinator or seed disperser has been lost or will not venture into the pasture (Cordeiro and Howe, 2003), or if its seeds will not germinate in a pasture, or if its seedling crop will be devastated by pasture-tolerant seedling predators, then it is among the living dead (Janzen, 1986): it will not replace itself, and, when it goes, so go the other species that used it.

Toward a (Protected) Role Within the Global Economy

Ecotourism has long been one of the most potent forces favoring conservation and will continue to be so. Ecotourists are consumers of services that nature provides (beauty, adventure, life lists, etc.), and they obligingly pay for these services in many ways (paying for park entry fees, rooms at hotels, vehicle repairs at the local mechanic, etc.).

But ecotourism is exceptional in these respects. The biosphere provides a steady stream of other direct and indirect benefits to humanity for which nobody pays. The last decade has seen "ecosystem services" transformed from an abstract academic concept (Ehrlich and Mooney, 1983) into an applied research program and a powerful policy tool (Daily, 1997; Millennium Ecosystem Assessment, 2005a). These services include, but are not limited to, providing raw materials, natural water filtration, carbon sequestration and storage in forests, flood and erosion mitigation by plant communities, and pollination of crops by wild animals (Daily, 1997). Ecosystems, in addition to being reservoirs of biological diversity and an integral part of our planetary and cultural heritage, are capital assets.

The global economy does not in any serious way account for the value of ecosystem services. The perversity of this situation is obvious. The costs, both in the traditional economic sense and in terms of human health and well-being, of losing these services would be immense: many economic institutions would either collapse outright or require technological surrogates vastly more expensive than simply conserving the relevant ecosystems. The archetypal example of an ecosystem service in action is the conservation of the Catskill watershed, which has (thus far) spared the city of New York the $8 billion cost of building a water-filtration plant. Elsewhere, there are indications that mangroves and other coastal vegetation might have protected some coastal villages from the devastating Asian tsunami of 2004 (Danielsen *et al.*, 2005). Recent population crashes of honey bees (*Apis mellifera*) have threatened an approximately $15 billion crop-pollinating industry in the United States, highlighting the importance of conserving diverse native-bee communities (Kremen *et al.*, 2002; Winfree *et al.*, 2007). These case studies are small components of a total-biosphere value that is, effectively, infinite (Dasgupta *et al.*, 2000).

The idea that economic growth is independent of environmental health, and that humanity can therefore indefinitely expand its physical economy, is a dangerous delusion. The problem is that although we know that individual ecosystem services are valuable, we rarely know precisely how valuable. And although quantitatively estimating the dollar value of individual services can be an eye-opening exercise, the effort required makes doing so prohibitive for every ecosystem (to say nothing of the futility of trying to add up to infinity). The challenges, then, are to provoke society to acknowledge ecosystem-service values (even though approximate or only qualitative) and to maintain service provision by protecting service sources.

In addition to the individual efforts of a growing number of academics and practitioners, innovative programs are emerging to tackle these twin challenges at large scales. The Natural Capital Project is an international collaboration involving Stanford University, The Nature Conservancy, and the World Wildlife Fund that aims to integrate ecosystem-service values into land-use and policy decisions (Aldhous and Holmes, 2007). By developing new decision-support tools—including software to quantify and map the value of ecosystem services across landscapes and seascapes—and applying them in several demonstration sites across the world, the project hopes to promote more forward-thinking land-use decisions.

In some cases, protecting ecosystem services (or even engineering them) may not enhance biodiversity conservation (Chan *et al.*, 2006; Turner *et al.*, 2007), but it may be useful for other anthropocentric reasons. We should be frank about that when pondering how to justify and finance our operations. We should also think about how increased valuation of ecosystem services might spill over into other sectors of the economy: If we rely on an ecosystem to do a job, are we putting a human being out of work, and might that person retaliate against the service-providing ecosystem?

Finally, we must recognize that, for whatever reason, demand for particular ecosystem services will wax and wane, but that the sources of the services must not be allowed to wax and wane in sync. As proponents and critics of market-based conservation approaches both point out, complete commodification of ecosystems is not the goal. Yes, ecosystem services have enormous value in traditional economic terms for their role in sustaining and enriching human life, and efforts to ascertain these values are important. No, ecosystems and their biodiversity cannot compete on the open market as service providers alone (Chan *et al.*, 2007). To subject ecosystems to all of the same demands and risks that commodities and corporations face in capitalist economies would be to ensure their eventual diminution and demise.

Globalization intensifies this hazard. In a globalized, demodularized world, goods and services can often be imported and outsourced more cheaply than they can be obtained locally—and this includes goods and services provided by ecosystems. ''Endemic'' ecosystem services, which cannot be supplanted by goods and services from distant sources, will likely be the most effective allies to biodiversity in the future.

Into Ecologically Reclaimed and Restored Habitats

Experience has shown not only that science can inform more rapid, more effective restoration of local habitats (Young *et al.*, 2005), but also that contiguous ecosystems can be built from scattered pieces at large scales

(Janzen, 2000). This process has several names—restoration, rewilding, renaturalization—and provides a constructive, creative counterpoint to the stop-loss approach of traditional conservation. Thus, the future of biodiversity is not just what we can save of what is left, but also what we can create from what is left [see also Soule and Terborgh (1999)]. As Young (2000) put it, "The conservation mindset is one of loss on a relatively short time horizon, whereas the restoration mindset is one of long-term recovery."

Successes abound. The regeneration of tropical forest in Guanacaste Province, northwestern Costa Rica (Janzen, 2000, 2002), is particularly heartening for several reasons: it involves restoration of multiple habitat types; it is large-scale yet local and decentralized; and it was achieved by using a portfolio of innovative mechanisms and via broad collaboration among scientists, businesspeople, politicians, and the local community. The result has been the regeneration and conservation of 700 km^2 of tropical dry forest along with abutting chunks of rain and montane forest. In poverty-stricken Niger on the fringe of the Sahara, farmers have helped hold off desertification in many areas by nurturing saplings in their fields rather than removing them—and they have begun to reap benefits from this greening of the countryside (Polgreen, 2007). In the oceans, researchers have had some success transplanting live coral fragments onto degraded reefs (Guzman, 1991). Likewise, efforts to rebuild damaged watersheds and wetlands have been a major focus of scientific restoration ecology [e.g., Mitsch and Wilson (1996)], with important implications for the availability of potable water.

Large animals are particularly extinction-prone, at both the population and species levels. They are also often particularly important to ecological dynamics. Returning megafaunal species to what remains of their historical ranges (Donlan *et al.*, 2006) can yield a number of overlapping benefits: the return of these charismatic species undoes population extinctions, makes habitats more interesting and exciting, and can restore ecological interactions with appealing systemwide consequences. The repatriation of wolves to Yellowstone National Park in 1995 not only titillated tourists but also revived a multispecies trophic interaction involving elk, beavers, and trees, which has rejuvenated the region's riparian ecosystems (Ripple and Beschta, 2007b; Wolf *et al.*, 2007).

These examples and others illustrate that ecological restoration has a critical role in determining where biodiversity goes from here; we hope for enormous and rapid expansion of such revival efforts, even if the ultimate ecological goals take centuries to achieve. The only caveat is that many projects branded as "restoration" may be only weakly beneficial or neutral for biodiversity (Zedler and Callaway, 1999). Tree plantations are not forests.

Into the Fabric of Local Communities

For various reasons, conservation programs in developing regions are likely to fail when they are imposed from the top down by outsiders/foreigners (Chapin, 2004). That realization has spurred interest in *(i)* involving local communities in conservation planning and *(ii)* fostering their desire and capacity to help achieve conservation goals. In some ways, these can be seen as short- and long-term components of the same strategy. Earning local support for a conservation initiative is needed to get the ball rolling; building local capacity ensures that the ball keeps rolling once the outsiders leave.

Community involvement in conservation planning and protected-area establishment/maintenance can take a variety of forms (Western and Wright, 1994; Borgerhoff Mulder and Coppolillo, 2005) and is the subject of a gargantuan literature. At its most straightforward, it involves dialogue and follow-up with local stakeholders to establish what kinds of compensation (broadly construed) would sweeten the prospect of restrictions on habitat use, but more nuanced and sophisticated schemes have also been used (Kremen *et al.*, 1999; Berkes, 2007).

Local capacity building can also operate at multiple scales. Education is clearly central to this goal, from providing on-the-ground biodiversity training in parataxonomy (Janzen, 2004b; Sheil and Lawrence, 2004) to training professional national park staffs to facilitating advanced degrees for local students via scholarships and other mechanisms (Rodriguez e*t al.*, 2007). But even more basic contributions (local-language publications and extension efforts, computer and telecommunications access, etc.) can be extremely beneficial.

As conservationists increasingly realize, programs along these lines should attend every tropical conservation effort. Such programs are crucial—not only for the long-term success of the given conservation effort, but also for the augmentation and transmission of biodiversity knowledge. Efforts to "engage" local communities in conservation and land management can and have gone awry, and there are often important tradeoffs between conservation and development (Chan *et al.*, 2007). None of this alters the fact that, without local acceptance of biodiversity and the rationale for its conservation, any gains will be ephemeral.

Onto the Cultural Radar Screen

For decades, conservationists have appealed to aesthetics as a principal reason to conserve wild areas and species. But beauty is in the eye of the beholder, and the 13-billion-plus beholding eyes of the world are drawn to many things that are hostile to biodiversity: large families, tractors, treasure, pavement, goats, and Cadillacs, to name a few. The processes of economic and infrastructural development help to divorce people from the natural world. Moreover, although outdoor recreation and ecotourism are still important parts of many lives in rich countries, biophilic impulses seem increasingly swamped by other stimuli. In the United States, the rise of electronic media has coincided with a 20-year downturn in National Park visitation, after 50 years of steady increase (Pergams and Zaradic, 2006). Recent findings indicate that similar declines in contact with nature are common to developed nations worldwide (Pergams and Zaradic, 2008).

Such trends will not be reversed and the biodiversity crisis will not be resolved until nature can rival virtual reality as a source of entertainment, intrigue, and inspiration. Janzen (2004a, 2005) offers a compelling analogy: as books are uninteresting and useless to an illiterate person, so is biodiversity uninteresting and useless to a bioilliterate person. People keep what they use, and increasing bioliteracy would enable more people to find uses for biodiversity. Demand for ecotourism and perceived "existence values" would increase and, with them, biodiversity-sustaining revenues. In a world of stingy appropriations for conservation, we have a wonderful academic literature on how to maximize returns on conservation investments (Wilson *et al.*, 2007). But we have spent comparatively little effort figuring out ways to create a world of biodiversity fanatics and conservation voters, where conservation resources would presumably flow more freely.

The earlier in the developmental process comes exposure to nature, the better the odds of inspiring devotion to biodiversity and its conservation. It is a rare conservationist who did not encounter nature as a child. Every one of us can go to elementary schools to show pictures of animals and plants and tell funny stories about ecology. The teachers will be happy to have us. More ambitious people might think about how to finance and institutionalize school field trips to natural areas. Those of us who work in the tropics can do these things there, too.

Clearly, we can also use other strategies. One method is to appropriate the very technologies that are currently enforcing the divide between people and biodiversity. Biodiversity is increasingly on the World Wide Web via projects such as the *Encyclopedia of Life* (www.eol.org) and *Wikispecies* (http://species.wikimedia.org). But we can do more. We can upload science and nature shorts to YouTube and contribute our knowledge to Wikipedia and its offshoots. We can post our lectures online (Rimer, 2007). We can work to add ecological dimensions to online virtual-reality platforms and video games like *Second Life*, which currently has 10 million registered accounts. These are obvious ideas; many more are possible.

There is hope here: Online sales have helped to revitalize classical music (Kozinn, 2006), which is like biodiversity in that its devotees have long been predicting and lamenting its demise.

Some have argued that the key to widespread biodiversity appreciation is the ability to know immediately what is what in nature. Janzen (Janzen, 2004a) believes that this requires a comprehensive library of DNA barcodes (Janzen *et al.*, 2005) along with a handheld, nanotechnological, field-portable sequencing device. We are hopeful about this dream, as well as any other means of achieving the same end.

Profound social transformations are not impossible or "unrealistic." Shifts happen. They have happened in our lifetimes. We all know these terms: segregation, Iron Curtain, apartheid. "Anthropogenic extinction" belongs on that list. More than anything else, the long-term future of biodiversity will be determined by our success or failure in helping to precipitate such an overhaul in popular perceptions of nature and what it means.

CONCLUDING THOUGHTS

A substantial amount of biodiversity—enough to preserve many functional ecosystems and to satisfy the desire felt by many to coexist with our only known living companions in the universe—can be saved via the pluralistic deployment of the seven sets of actions that are discussed above and that have been discussed for years in countless other corners of academia.

The subheadings sound ambitious, but the actions they comprise are demonstrably doable. As with the atmospheric "stabilization wedges" of Pacala and Socolow (2004), each of the strategies above has passed beyond the laboratory bench and demonstration phase, but none has yet been implemented on a large-enough scale or in conjunction with enough of the others. Part of the reason for this shortfall is that most of us in the academic community who are familiar with all of these ideas do not see implementing them as part of our job description.

Where Does Conservation Biology Go from Here?

Academic ecological papers are often tinseled with one or two sentences about the applied significance of the science (Marris, 2007), which accomplishes little. The selective pressures of academia, as currently set up, promote this practice by insisting on work that is at once scientifically transformative and socially beneficial. Yet many of the most useful things that we can do for biodiversity—like talking to kindergartners—are not at the cutting edge of science. Thus, we are implicitly encouraged to deck our papers with references to the urgent biodiversity crisis while quietly opting out of the grittier work. (We do not excuse ourselves from this indictment.)

This phenomenon is the very definition of the Ivory Tower, but it need not apply here. It is up to us. We can maintain the status quo, which has not yet enabled us to stop or even slow biodiversity loss. Alternatively, we can go a few steps down from our cathedral by systematically rewarding (or even mandating) a certain tithe to society and incorporating it into our system for evaluating one another. Each institution seems free to make its own decision on this front. Major funding bodies, such as the U.S. National Science Foundation, rightly insist that applicants explain both the intellectual importance and the "broader impacts" of their science. However, we suspect that scientists face more accountability to the former than to the latter. Closer scrutiny of the delivery of societal benefits promised from previous grants would likely prompt an increase in tithing.

Where Does Humanity Go from Here?

Where the human juggernaut goes from here will depend in many ways on where biodiversity goes. In this chapter we have tried to suggest one hopeful answer: from here, humanity goes to grips with biodiversity as a part of society that we accept, accommodate, need, use, pay for, puzzle over, admire, and enjoy. The alternative future is much uglier, but we still have time to reject it.

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