

In the light of evolution II: Biodiversity and extinction

John C. Avise*†, Stephen P. Hubbell‡, and Francisco J. Ayala*†

*Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697; and †Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095

The Earth's biodiversity is a well-spring 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 (2), 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 (3, 4). The last catastrophic extinction, which occurred ≈ 65 million years ago and was the *coup-de-grace* for non-avian 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 $\approx 50,000$ – $100,000$ 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 (5) estimated that the Earth is currently losing $\approx 0.25\%$ 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, policy makers, 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.

The goals of this Colloquium were to synthesize recent scientific information and ideas about the abundance and distribution of biodiversity and to compare contemporary biodiversity and extinction patterns with those in the distant and near evolutionary past as well as with those plausible in the near-term future. Articles from the Colloquium address biodiversity and extinction in four contexts: *Contemporary Patterns and Processes in Animals*; *Contemporary Patterns and Processes in Plants and Microbes*; *Trends and Processes in the Paleontological Past*; and *Prospects for the Future*.

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 articles under this heading, and the next, illustrate some of the challenges of quantifying the magnitude of extant biodiversity and deciphering extinction rates and patterns in a representative selection of diverse contemporary biotas.

Oceans cover three-quarters of the Earth's surface, and their inhabitants might seem at first thought to be somewhat buffered (compared with terrestrial and freshwater species) against anthropogenic disturbance. However, Jeremy Jackson (6) 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.

David Wake and Vance Vredenburg (7) describe a similarly gloomy scenario for the global status of amphibians. Of

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†To whom correspondence may be addressed. E-mail: javise@uci.edu or fjayala@uci.edu.

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the $\approx 6,300$ 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. Approximately 70% of coral reefs globally have been degraded beyond recognition in recent years (20%), are in imminent danger of collapse (24%), or are under longer-term threat of demise (26%) (8). Marjorie Reaka *et al.* (9) 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. Andy Dobson *et al.* (10) 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 $\approx 10\text{--}15\%$ of parasitic helminthes (Trematoda, Cestoda, Acanthocephala, and 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.

Contemporary Patterns and Processes 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 after the arrival of humans and their hitchhiking associates. Dov Sax

and Steven Gaines (11) 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 *et al.* (12) illustrate by applying neutral biodiversity theory (13) to estimate the number, abundance, range size, and extinction risk (under alternative scenarios

Box 1. In the Light of Evolution. In 1973, Theodosius Dobzhansky penned a short commentary titled "Nothing in biology makes sense except in the light of evolution" (25). 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. 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 challenges, as well as 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 agricul-

ture, pharmacology, and biotechnology. The ramifications of evolutionary thought extend into learned realms traditionally reserved for philosophy and religion. The central goal of the *In the Light of Evolution* series will be to promote the evolutionary sciences through state-of-the-art colloquia and their published proceedings. Each installment will explore 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 *In the Light of Evolution* series will aim 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 (J.C.A. and F.J.A.) are the academic grandson and son, respectively, of Theodosius Dobzhansky, to whose fond memory this *In the Light of Evolution* series is dedicated. May Dobzhansky's words and insights continue to inspire rational scientific inquiry into nature's marvelous operations.

of future habitat loss) for medium- and large-sized trees in the Amazon Basin. Their quantitative analysis suggests that >11,000 tree species inhabit this extraordinarily biodiverse region. The good news for biodiversity conservation is that >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 (>5,000 species likely to consist of <10,000 individuals each) estimated near-term extinction rates are 37% and 50%, respectively, under optimistic and nonoptimistic 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. Jessica Bryant and colleagues associated with Jessica Green (14) tackle such problems on a mesogeographic 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 (nonrandom 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 (15) would like to see rectified. These authors review experiments and observations from the scientific literature to address questions about the composition of a microbial community after 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 predisturbance 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.

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 articles 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 (≈ 440 mya), Devonian (370 mya), Permian (245 mya), Triassic (210 mya), and Cretaceous (65 mya). Each was characterized (indeed identified) by a substantial loss of then-extant taxa. Douglas Erwin (16) 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 (17) develops a somewhat similar theme 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 after 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.

John Alroy (18) 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-myrr 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 >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. Anthony Barnosky (19) 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 transi-

tions 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.

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? Articles 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. Michael Donoghue (20) 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 (21) show how a phylogenetic modeling approach can help to identify mammalian taxa whose intrinsic biology might make them especially vulnerable to environmental pressures. They begin by combining phy-

logenetic 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, John Avise (22) 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.

Michael Novacek (23) 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 the closing article of this Colloquium, Paul Ehrlich and Robert Pringle (24) remind us that “the fate of biological diversity for the next ten 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.

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. 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. Little time remains for the public, corporations, and governments to awaken to the magnitude of what is at stake.

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