Declines of biomes and biotas and the future of evolution

David S. Woodruff*

Ecology, Behavior, and Evolution Section, Division of Biology, University of California at San Diego, La Jolla, CA 92093-0116

Although panel discussants disagreed whether the biodiversity crisis constitutes a mass extinction event, all agreed that current extinction rates are 50–500 times background and are increasing and that the consequences for the future evolution of life are serious. In response to the on-going rapid decline of biomes and homogenization of biotas, the panelists predicted changes in species geographic ranges, genetic risks of extinction, genetic assimilation, natural selection, mutation rates, the shortening of food chains, the increase in nutrient-enriched niches permitting the ascendancy of microbes, and the differential survival of ecological generalists. Rates of evolutionary processes will change in different groups, and speciation in the larger vertebrates is essentially over. Action taken over the next few decades will determine how impoverished the biosphere will be in 1,000 years when many species will suffer reduced evolvability and require interventionist genetic and ecological management. Whether the biota will continue to provide the dependable ecological services humans take for granted is less clear. The discussants offered recommendations, including two of paramount importance (concerning human populations and education), seven identifying specific scientific activities to better equip us for stewardship of the processes of evolution, and one suggesting that such stewardship is now our responsibility. The ultimate test of evolutionary biology as a science is not whether it solves the riddles of the past but rather whether it enables us to manage the future of the biosphere. Our inability to make clearer predictions about the future of evolution has serious consequences for both biodiversity and humanity.

The science of evolution, linked to the related sciences of ecology, paleobiology, and genetics, seeks to explain the history of life on earth. After about 150 years of formal inquiry, we seem to be more than half way to accounting for the development of biomes and biotas, the biosphere, and ourselves. We can now account for much of the past and present in terms of genetics, ecology, and chance. However, the real measure of a science's maturity is its ability to make sound predictions about the future. Our discussion of the future of biomes and biotas, even with one of the colloquium organizer's contributions (1–3) as a guide, revealed that we are frankly unequal to this challenge despite its urgency. Our inability to make clear predictions (beyond sweeping generalizations) about the future of life on earth has serious consequences for both biodiversity and the well being of humanity. In the last 50 years, it has become widely accepted that the eruption of the human population is causing the extinction of much cherished biodiversity and is altering biosphere-level processes that we depend on for $3–33 trillion worth of environmental services annually (4, 5). Our population density is now >30 times that predicted for an omnivorous mammal of our size, and it has been estimated that we usurp >40% of the planet's gross terrestrial primary productivity to our own ends (6, 7). If our greatest achievement in the last century was the collective understanding of what evolution and its products, the biosphere, mean to our own survival, the challenge of the present century is to develop a more predictive science of evolutionary ecology before it is too late to shape a desirable future.

There is no doubt that the biodiversity crisis is real, and upon us, and began roughly 30,000 years ago (8). We speak with less scientific assurance, however, about almost every one of the widely quoted numbers describing its magnitude and significance. Nevertheless, we live at a geological instant when global rates of extinction are at an all time high for the last 65 million years (My) and are increasing. Most extinctions go unrecognized; thus, estimates of overall rates have high errors. Currently, however, several million populations and 3,000–30,000 species go extinct annually of a global total of >10 million species (9, 10). Probably at least 250,000 species went extinct in the last century, and 10–20 times that many are expected to disappear this century. Although we can identify the most threatened biomes and species in some groups [ref. 11; see World Conservation Union (2000) at http://www.redlist.org], we cannot make acceptably rigorous predictions about the consequences of these extinctions for the future evolution of life or for the integrity of the biosphere's environmental services that we still take for granted.

The taxonomic course of the biodiversity crisis is reasonably understood for terrestrial vertebrates and a few other groups (11). In the last few centuries, we have lost one family of mammals (Nesophontidae), half the birds of Hawaii, possibly the most common bird in North America (the passenger pigeon), and all of the moas—a total of 1,139 documented plant and animal species globally. Further, we have extirpated most of the fish in the lakes of the northeastern United States and most of the primates from the remaining forests of West Africa. The situation in the oceans is poorly known but comparable or worse (12). If we step back 30,000 years, we have contributed to the elimination of the megafauna of the Holarctic, Neotropics, and Australian zoogeographic regions (70 species and 19 genera of mammals in North America); these extinctions involve the disappearance of several other families of mammals (13). Today's taxon-specific global extinction rate estimates are 50–500 times background, and half the remaining vertebrates are at risk of extinction, including most whales and primates. Already >30 species of mammals and birds survive only because of the intensive care they receive in zoos and nature reserves. Taxon-specific assessments of threat have been prepared by the Conservation Breeding Specialist Group of the World Conservation Union (IUCN) for many groups ranging from palms to parrots to *Papilio*, the swallowtail butterflies.

Lamentable as these expected species losses are, it has been argued that even if we lose 90% of the species on the planet, we

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may lose only 20% of the phylogenetic diversity (14). This claim can be made, because in most genera, there are several species, and the survival of one, it is argued, may capture most of the genetic variability of the whole clade. Although this estimate is controversial, it explains why some question whether we should be saving rare species in species-rich clades. Is one tuatara worth 200 species of skinks? Are rare species treasures or dross (15) from an evolutionary point of view? However, saving phylogenetic diversity is not currently the goal of global conservation efforts, and science does not yet clearly indicate that it should be.

The ecological consequences of our destruction of biomes and biotas are understood in broad generality as they impact human well being locally and regionally. Less clear are the global implications of habitat destruction, especially species-rich tropical forests, wetlands, and coral reefs (16). Predictions are complicated further by the recent realization that human activities are altering climates globally. The exploration of Sala and coworkers (17, 18) of the impact of various drivers of change (and the interactions between these drivers) on global ecosystems and biodiversity loss in the year 2100 illustrates both the power and the current limitations of scientific inquiry at this level of concern. Nevertheless, there is general agreement that the biosphere will have fewer species and be subject to more weed, pest, and disease outbreaks. Heretofore dependable nutrient cycles may become less predictable as essential microbes succumb to anthropogenic toxins. The new biomes will be more easily disturbed and invaded, and will have an aesthetically unappealing dullness. In considering these generalities, the discussants agreed on one thing: evolution will continue as the major driver or cause of biodiversity. Although we are ushering in a period of geological time characterized by the homogenization of biotas (19, 20), dubbed the Homogecene at this meeting, the basic processes causing evolution will continue. Evolution is not over—set back perhaps—but by no means over.

In answer to the question, "Is the biodiversity crisis unprecedented?" there was also general agreement: no. There was, however, surprising debate as to whether it warrants being called a mass extinction event. Recall that a 1998 Harris (21) poll found that 70% of biologists asked said they believed a mass extinction was underway and accepted that 20% of all species will go extinct in the next 30 years (22). This issue arose when I asked the discussants to continue the diversity line on a standard Sepkoski plot of marine invertebrate families over the last 600 My to the year 3000 to show a predicted 50% loss of species. Would one expect the line to fall to 40% or to 60% of today's all time high level? Jablonski and other discussants argued that it might only drop 1% and therefore the biodiversity crisis is absolutely not a mass extinction event.

This difference of opinion is both important and potentially dangerous. Mass extinction events are typically defined in terms of their irreversible impact on large numbers of species in diverse taxa on a global scale in a short period. In five previous events, 15–90% of the marine invertebrate species studied went extinct (23, 24). However, today, marine species account for only about 15% of biodiversity (25), and we are most concerned with losing terrestrial species rather than higher level taxa. Thus, attempts to show the magnitude of the current extinction event on a plot of marine invertebrate families is inappropriate and dangerous in that it belittles its significance. Unfortunately, the comparable multitaxon plot of species numbers through time is not yet available; when it is, we will be able to illustrate graphically the probable impact of the current event in comparison with the previous big five marine invertebrate mass extinctions. A hint of what this impact might look like is provided by Alroy's studies of North American mammal species through the last 98 My (26). The end-Pleistocene extinction rate of 32% is already as extreme as any other during the previous 55 My but does not yet approach the 76% rate observed at the Cretaceous–Tertiary boundary

(27). Regan *et al.*'s (28) contribution to the problems of estimating global extinction rates and the use of fuzzy arithmetic to consider multiple uncertainties appeared after this colloquium.

My personal opinion is that we are currently living in what will eventually be recognized as a real mass extinction. If current area-species curve-based projections are correct, we could lose up to 50% of the planet's species in the next 1,000 years. Raup's consideration of the number of species in genera, and of genera in families, across phyla, shows that a 50% loss of species may involve a 25% loss in genera and a 10% loss in families (29). Furthermore, extinctions do not occur at random in space and in clades. The losses will be higher in the tropics, because the species/genera ratio changes with latitude (30). Purves *et al.* (11) show clearly that the nonrandom phylogenetic losses of mammal and of bird species since 1600 are already equivalent to the loss of one monotypic phylum. The authors estimate that an additional 120 genera of mammals and birds are at risk over expectations under random extinctions. Regardless of whether such calculations qualify the current biodiversity crisis as a mass extinction event, we all agreed that it would be inexcusable to let it become one (or a worse one). To this end, we reached conclusions that may be summarized here as: arm the scientists, alert the public, and do anything to buy time.

Causes of the Decline in Biomes and Biota

The causes of the biodiversity crisis are well known and include human impacts on habitats (habitat destruction, degradation, fragmentation, and restructuring) and on organisms (overexploitation, introduction of exotic competitors, predators and parasites, and creating new pests) (8, 10, 31, 32). Discussants noted differences in geographic rates of habitat alteration and destruction (largely complete in Europe and North America and on-going in the tropics) and that such rates are unprecedented in the tropics and subtropics in the Neogene. There was agreement that community simplification (with loss of pollinators and dispersers) and the regional homogenization of biotas, with weedy opportunists replacing endemic specialists, are of serious concern. The well recognized vulnerability of island biotas will be exacerbated by our accelerated importation of parasites and predators. The introgressive hybridization of cultivars and their "wild" ancestors was noted as also requiring more attention, because it can lead to the evolution of aggressive weeds and the extinction of rare species (33). Potential threats from transgenic genetically modified organisms will require vigilance and careful assessment (34).

In coinciding with a period of rapid anthropogenic global warming, the biodiversity crisis could not have come at a worse time. The rate of warming is unusually fast but not without precedent (35). Further, most living species have experienced global temperatures as warm as today's for <5% of the last 2–3 My (36). Orbitally forced species range dynamics associated with 100,000-year Milankovich cycles have caused repeated changes in the distributions of most temperate zone species (37, 38) and caused ranges of some North American species to shrink progressively with successive cycles (13). The ability of species to respond to future climatic oscillations by range shifts will be greatly reduced by our creation of an inhospitable matrix between the remaining habitat patches. We can no longer expect many terrestrial temperate zone species to shift naturally 1,000 km pole-ward at $CO_2 \times 2$, when mean global temperatures are predicted to be 5°C above today's. Increased nitrogen will also have significant impacts on soils, plant productivity, and biodiversity (39).

Future of Evolutionary Processes

All predictions about the future of life on earth and about the >10 million species and their various assemblages involve two pivotal assumptions about a single species, our own. The first

assumption concerns human numbers and provides a simple metric of the impact of our population. The second assumption concerns our per capita consumption of natural resources, food, and energy. Discussion of the future of evolution presupposes the availability of acceptable 100-year and 1,000-year projections for human populations. The 100-year prediction is reasonably clear and leads to a consensus view of a warmer world with many more species missing, with the survivors living in fragmented habitats and losing genetic variability fast, and with "wilderness" a largely historical state of nature. However, "reasonable clear" is misleading, because the human population could reach as high as 16 billion, or it could peak at 7.5 billion around 2040 and return to 5.5 billion by 2100 (40). Not surprisingly, the 1,000-year projections for human numbers and behavior are too speculative to print; however, it is already clear that we cannot expect a return to a prebiodiversity crisis state of nature under even the most favorable scenarios with reduced human impact. Recovery from previous mass extinction events has taken 5–10 My (41, 42). Action taken in the next few decades will determine how impoverished the biosphere will be in 1,000 years. By then, many surviving "wild" species will require active maintenance by wildlife managers using ecological and genetic methods yet to be developed, in a world dominated by species commensal with humans. Discussion focused on the origin of "commensals"—from where do they come? from hot spots or disturbed areas? from what clades? from what biomes? Under even the most favorable speculations about the 1,000-year situation, there was serious concern about the ability of biodiversity to "bounce back" given the current prospects for tropical forests, wetlands, and coral reefs.

The consequences for biotas over the next 100 years are easier to predict.

Species Geographic Ranges. One of the lessons of paleobiology is that a species geographic range is a good indicator of its probability of surviving mass extinction events, ice ages, and other major environmental changes (see refs. 13, 23, and 43). Of particular interest is the response of individual species to global climate change and the probability that new species assemblages will form, analogous to the "disharmonious" communities of the Late Pleistocene. In the past, single species and interacting species have moved rather than adapted to such change, but such dispersal will no longer be possible. In future, terrestrial species will have to adapt or their dispersal will have to be managed, especially in plants and other low-vagility organisms. Ironically, this realization comes just as progress is being made on one of the great puzzles of the Modern Synthesis, the evolution of species ranges (44), on how climate change leads to both local adaptation in peripheral populations and range shifts (45). Gene flow is predicted to increase in commensal species and decrease in natives as their ranges become fragmented. Spatial heterogeneity will therefore decrease in commensals and increase in natives. Templeton (46) argues that range fragmentation will lead to extinction and not speciation, because the individuals in fragmented populations will not increase in numbers fast enough for divergence to occur. Managers will have to move the proverbial one individual per generation between remnant subpopulations of metapopulations to counter genetic drift (47). The possibility that habitat fragmentation may actually increase rather than decrease gene flow and population genetic variation, as found recently in *Acer* (48), needs further examination. Studies of probable adaptive responses of individual species to global warming are in their infancy (e.g., ref. 49).

Genetic Aspects of Risk Assessment. Although the ecological and behavioral characteristics associated with high extinction risk are reasonably well understood (but only in a few taxa), the population genetic components of viability are also receiving atten-

tion (50). Genetic drift is expected to decrease in the growing populations of commensals and increase in the fragmented and smaller populations of natives. Genetic risks that were largely ignored in the last century will become dominant concerns in a world of small, recently isolated populations with declining genetic effective population sizes, N_e. Genetic erosion, the decrease in population variation caused by random genetic drift and inbreeding, is both a symptom and a cause of endangerment of small isolated populations (51). The phenomenon has been long understood in terms of population genetic theory (47); however, the devastating early stages of the process in nature have gone undocumented, because the changes are rapid [under standard models heterozygosity declines at $1/(2N_e)$ per generation; ref. 47] and difficult to monitor. Recently, a method for monitoring genetic erosion based on noninvasive genotyping using nuclear microsatellite variation has been introduced (52). Our studies showed that, although genetic erosion accompanied habitat fragmentation and demographic collapse in some species, the process apparently can begin before detectable demographic decline of local populations of other species (52). This finding is important, because genetic studies of threatened populations usually are performed only after demographic studies indicate that there is a problem. In the future, managers will have to survey both demography and genetics, and their interaction, to assess a fragmented population's viability. In addition to genetic drift, inbreeding can also threaten a fragmented population's viability (53), and again, recent application of molecular genetic assays provides a clear demonstration of its impact on extinction in nature (54). The implication of these observations is that wildlife managers will increasingly have to intervene; nature can no longer be left alone to function, because our actions have doomed countless isolated populations to slow genetic decline and extirpation.

Genetic Assimilation. The threats of genetic swamping of rare species by common congeners are seen as increasing (33). Molecular genetic methods now permit the detection of earlier incidents of genetic assimilation that have extirpated or exterminated one of the hybridizing taxa. The assimilated taxon remains as a phantom in the gene pool of the surviving species whose variability is enhanced by the interaction. Whether this increased variability increases its evolvability is not known, but it may. This issue is relevant to the more frequently confronted circumstance involving threatened polytypic species and superspecies: is it preferable to save a single "generic" taxon or several separate subspecies? Existing theory does not give a clear general answer.

Natural Selection. As a bold generalization, selection pressures on commensals are predicted to increase, largely as a result of artificial selection. Similar increases in selection pressures on populations of natives are also expected, but largely through the agent of natural selection. There was general agreement that selection intensities will increase because of environmental changes. Tilman (39) discusses selection for dispersal, competitive ability, and plasticity. The relationship between community simplification, disturbance and invadability, and selection pressures on small populations needs more attention. Selection at the ecosystem level (55) was not discussed, but it is predicted that the proportion of *r*-selected species will increase and that the number of pest species will probably double.

Mutation Rates. Mutation rates may rise as a result of increases in background mutagen concentrations, increases in UV-B caused by ozone depletion by N_2O and chlorofluorocarbons, and locally significant nuclear waste storage. Lande (56) has argued that, even without any increase in mutation rates, the viability of many populations will become increasingly compromised. The rate of

production of quasineutral, potentially adaptive genetic variance in quantitative characters is an order of magnitude smaller than the total mutational variance, because mutations with large phenotypic effects are typically detrimental. The effective population size should be about 5,000 to maintain normal adaptive potential in quantitative characters under a balance between mutation and genetic drift (or among mutation, drift, and stabilizing natural selection). In populations below this effective size, the risk of extinction because of the fixation of mildly deleterious mutations may be comparable in significance to environmental stochasticity and may substantially decrease long-term population viability.

Reflecting the expertise of the participants, our discussion focused less on the consequences for biomes and for ecosystem functions over the next 100 years (ref. 57 and other articles in this colloquium). Concerns were voiced over unknown thresholds and altered states affecting biogeochemical cycles, about increases in emergent diseases and pest eruptions, and about the significance of the loss of keystone species. We also noted the possibly disproportionate loss of morphological and ecological variety or disparity (58). More discussion focused on food webs, on the shortening of food chains, on patterns of connectedness, on redundancy, and on the increase in nutrient enriched niches permitting the ascendancy of the microbes. Some previous mass extinction events were apparently followed by a period when microbial mats were prominent and by the differential survival of widespread ecological generalists. There is far too little realization, even among conservation mangers, that many of the species in trouble today are in fact already members of the doomed, living dead (59). As Janzen has remarked, perhaps we should adopt the principle that species are extinct until proven extant rather than the other way around as currently practiced.

In summary, it is clear that the rates of basic evolutionary processes are being altered. More significantly, the ecological theater in which these agents operate will change dramatically as species disappear. The players, the species, will change in character, with 50% of the natives disappearing and the invasives (currently 2% of biota), domestics (currently 1%), and locally expanding species (currently 5–29%) becoming dominant over most of the globe (19, 20). Such homogenization of biotas is without precedent in the last 65 My. Microevolution will increase in commensals and increase or decrease in natives depending on circumstances and time frame. There will be multiple new constraints on adaptation. For speciation rates, no change or increases associated with empty niches are expected for commensals, and net decreases are predicted among surviving natives (43). Although sexual selection may rapidly produce the kind of reproductive isolation associated with speciation in some fragmented populations (60), the overall trend will be toward extinction. Speciation in the large vertebrates is essentially over for the foreseeable future. Speciation may pick up again in the more distant future if isolated allopatric populations are large enough and survive long enough to diverge, or empty niches can be filled. Avise (61) has argued that numerous incipient species lie waiting as genetically differentiating populations after the last glacial phase and that, with time, they may produce a burst of originations. Again, this "burst" is more likely to occur on time scales of 10^4 to 10^6 years than the 100–1,000 years under consideration, but there are an increasing number of examples of more rapid speciation (62–64). Current global speciation rates are estimated to be <1 per year or four orders of magnitude less than the extinction rate (65). Extinction rates themselves should, as noted above, decrease for commensals and increase differentially for natives. Natural recovery will take millions of years and be largely unpredictable in its details. Predictions using quasineutral, potentially adaptive mutations to estimate the effective population size necessary to maintain evolvability indicate that setting goals involving <10^4 individuals are inadequate. Below this size, we will have to engineer evolvability to ensure long-term viability. Bioneering, the interventionist genetic and ecological management of species, communities, and ecosystems in a postnatural world, is poised to become a growth industry. It is not the control of nature that we should seek but rather a deeper appreciation of the natural dynamics of these complex systems and a willingness to work with rather than against these dynamics (66). Although many of the above predictions are frankly speculative, there was general agreement that the biosphere in the year 2100 will be less predictable and that events then will unfold at rates traditionally labeled as "unpleasant surprises." Myers' (67) precautionary principle and Wilson's (68) admonition about the one thing (loss of biodiversity) our descendents are least likely to forgive us for are basic maxims guiding our response to the biodiversity crisis. Evolutionary processes will continue but with results that are increasingly difficult to predict.

Recommendations

The discussants identified 10 recommendations for policy, research and education. These include two of paramount importance, seven identifying specific activities to better equip us for the stewardship of the processes of evolution, and one suggesting that such stewardship is now our responsibility.

1. Promote efforts to reduce human population growth and resource use, because conservation goals cannot be achieved without addressing human needs and aspirations.
2. Promote the teaching of ecology and evolutionary biology in the educational process at all levels.
3. Promote efforts to complete a rapid inventory of the planet's biota, including Species 2000 and the Global Biodiversity Information Facility, to provide these foundational data in 20 years rather than 600 years, at present rates of activity (69–71). We also need to establish the true evolutionarily significant units in the few hundred species we select for intensive management and protection, of the >10^4 species that will need interventionist management by 2100 (72, 73).
4. Promote research on landscape- and on seascape-level processes so as to improve fundamental species level conservation.
5. Foster research on the predictive use of the fossil record. If the past has taught us anything, it is that evolution is a hierarchical process (74) that cannot be predicted beyond some crude generalizations. Paleobiology promises to give us the perspective to assess and react to the biodiversity crisis scientifically.
6. Promote research on the relationship between genetic variability and population viability and ultimately evolvability (50, 53). Most evolutionary and conservation biologists assume that increasing genetic variance always enhances the probability of population survival and evolution, but this assumption is not generally true (75). In constant and unpredictable environments, genetic variance reduces population mean fitness. In predictable, highly variable environments, genetic variance may be essential for adaptive evolution and population persistence. Because almost all predictions point to natural populations losing genetic variability, we may need to reexamine Fisher's Fundamental Theorem in the light of advances in understanding of the genetics of quantitative and quasineutral trait evolution. Also the possible conversion of nonadditive genetic variance to additive variance in small populations leading to increased variance in fitness needs more study, as does the issue of genetic load, which takes time to evolve and is still difficult to detect experimentally (76). If most new variation so

produced is deleterious, or mildly deleterious, then perhaps these concerns can be set aside in the short term.

7. Promote research on genetic control of pests and their vectors to diminish their importance in disturbed ecosystems and improve the human condition (e.g., ref. 77).

8. Promote the development of a global system of nature reserves especially in the tropics. The current IUCN goal of 10% national set-asides to represent each biome and the latest proposals to focus efforts on biodiversity hot spots (a Global 200 and a Global 25, among others) all deserve encouragement, because they will save biomes and biotas more effectively than single species conservation efforts (78–80). The arguments for greater cooperation between the various stakeholders (academic, nongovernmental, governmental, and local communities) and for better science in setting global priorities should be heeded (81, 82), but scholarly debates among ourselves about the weaknesses of any one proposal are counterproductive if they delay action. Solutions offered by scientists will almost always be compromised in their application to the real world by reasonable human rights concerns, and furthermore, the sooner we move beyond parks and reserves in our planning, the better (83, 84).

9. Promote political, legal, and regulatory changes to redesign and recommission existing protected areas so that they may better conserve their native biotas in the face of climate change, edge effects, and increased demand for sustainable use by local people and recreational use.

10. Finally, some of us advocate a shift from saving things, the products of evolution, to saving the underlying process, evolution itself (46, 72, 85). Facilitating this process will ultimately provide us with the most cost-effective solution to the general problem of conserving nature. The human predicament requires that we accept responsibility for this process and its products. Like it or not, evolutionary biologists have to recognize that the ultimate test of their science is not their ability to solve the riddles of the past and the origin of species, but rather to manage their viability and prevent their premature extinction, to manage the biosphere's future. In this sense, if they turn around and face forward in time, evolutionary biologists become conservation scientists. The traditional dichotomy between one group doing fundamental research and the other doing applied work is false. Conservation biology provides some of the most difficult problems ever tackled by science—difficult because of their complexity and because many cannot be approached with the reductionist methods that served us well in other fields. Because these problems affect the viability of our own species and the biosphere generally, there is no more significant scientific challenge demanding our attention this century. "If, then, we wish for evolution to proceed in ways that we consider progressive we ourselves must become the agents to make it do so. And all our studies of evolution must finally converge in that direction" (86). Nowadays, we would never use the word "progressive," but the challenge remains valid and more urgent.

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