The current biodiversity extinction event: Scenarios for mitigation and recovery

Michael J. Novacek*[†] and Elsa E. Cleland[‡]

*American Museum of Natural History, New York, NY 10024; and [‡]Department of Biological Sciences, Stanford University, Stanford, CA 94305

The current massive degradation of habitat and extinction of species is taking place on a catastrophically short timescale, and their effects will fundamentally reset the future evolution of the planet's biota. The fossil record suggests that recovery of global ecosystems has required millions or even tens of millions of years. Thus, intervention by humans, the very agents of the current environmental crisis, is required for any possibility of short-term recovery or maintenance of the biota. Many current recovery efforts have deficiencies, including insufficient information on the diversity and distribution of species, ecological processes, and magnitude and interaction of threats to biodiversity (pollution, overharvesting, climate change, disruption of biogeochemical cycles, introduced or invasive species, habitat loss and fragmentation through land use, disruption of community structure in habitats, and others). A much greater and more urgently applied investment to address these deficiencies is obviously warranted. Conservation and restoration in human-dominated ecosystems must strengthen connections between human activities, such as agricultural or harvesting practices, and relevant research generated in the biological, earth, and atmospheric sciences. Certain threats to biodiversity require intensive international cooperation and input from the scientific community to mitigate their harmful effects, including climate change and alteration of global biogeochemical cycles. In a world already transformed by human activity, the connection between humans and the ecosystems they depend on must frame any strategy for the recovery of the biota.

There is consensus in the scientific community that the current massive degradation of habitat and extinction of many of the Earth's biota is unprecedented and is taking place on a catastrophically short timescale. Based on extinction rates estimated to be thousands of times the background rate, figures approaching 30% extermination of all species by the mid 21st century are not unrealistic (1–4), an event comparable to some of the catastrophic mass extinction events of the past (5, 6). The current rate of rainforest destruction poses a profound threat to species diversity (7). Likewise, the degradation of the marine ecosystems (8, 9) is directly evident through the denudation of species that were once dominant and integral to such ecosystems. Indeed, this colloquium is framed by a view that if the current global extinction event is of the magnitude that seems to be well indicated by the data at hand, then its effects will fundamentally reset the future evolution of the planet's biota.

The devastating impact of the current biodiversity crisis moves us to consider the possibilities for the recovery of the biota. Here, there are several options. First, a rebound could occur from a natural reversal in trends. Such a pattern would, however, require an unacceptably long timescale; recoveries from mass extinction in the fossil record are measured in millions or tens of millions of years (10). Second, recovery could result from unacceptably Malthusian compensation—namely, marked reduction in the world population of human consumers. Third, some degree of recovery could result from a policy that protects key habitats even with minimal protection of ecosystems already altered or encroached on by human activity (i.e., protecting "hotspots"). A fourth recovery scenario involves enlightened human intervention beyond simple measures of wilderness preservation, a strategy that embraces ecosystem management and mitigation of the current alteration of global biogeochemical cycles. Here, strong preference is expressed for the last of these options. Clearly, the future of evolution of the planet's biota depends significantly on what we do now to minimize loss of species, populations, and habitats. At the same time, there is acute recognition of the challenges and potential shortcomings of many attempts at remediation and recovery. It is hoped that this panel's consideration of major threats, their interaction, and the linkage between science and conservation in mitigating these threats suggest some feasible recovery scenarios at several different scales.

Lessons from the Past: Recovery as a Long-Term Phenomenon

It is clear that the fossil record powerfully indicates the reality of extinction on many scales, the magnitude as well as selectivity of effects, and the pattern of recovery and survival (11, 12). To what extent then does the fossil record help us in forecasting both scenarios for extinction and recovery in the current crisis? Consideration of this question moves us to acknowledge that there are several aspects of these past events that diminish their relevance to the current situation.

First, ancient mass extinction events have been documented over comparatively long or imprecise timescales. The current crisis has been extended through historical times, a matter of centuries or a millennium, with a greatly accelerated impact that began during the 20th century with the exponential increase of world human populations. Thus, a period of only 75 to 100 years may be most critical to the transformation of the present biota.

Second, mass extinction events of the past are typified by global scale ecological transformation. By contrast, the current event is typified by a "patchy" pattern involving habitat fragmentation and loss, where impacts vary markedly for different habitats and different regions of the world (13). There is a large body of evidence that suggests global climate changes and alteration of global biogeochemical cycles may cause widespread transformations of ecosystems, but significant biodiversity loss has not yet been linked to these impacts.

Third, data on mass extinction events in the fossil record often fail to provide a clear connection between a primary cause and effect (14–16). In contrast, the current biodiversity crisis has one obvious biotic cause: ourselves. Moreover, the source of the trauma also has the presumed capacity to mitigate its own deleterious impact. Although the extinction of many species may be an irreversible outcome of the current event, certain aspects of human-caused global change are reversible.

This paper was presented at the National Academy of Sciences colloquium, "The Future of Evolution," held March 16–20, 2000, at the Arnold and Mabel Beckman Center in Irvine, CA.

[†] To whom reprint requests should be addressed. E-mail: novacek@amnh.org.

www.pnas.org/cgi/doi/10.1073/pnas.091093698

All of the above distinctions are pertinent to any scenario for recovery that might be extracted from fossil and geological evidence. Various reviews suggest that replenishment and diversification of the biota following mass extinction events required a recovery phase of millions or tens of millions of years (10, 12, 15). Surely such estimates based on fossil data indicate the time lag that might be expected for a natural recovery of the biota following the current extinction event. Nonetheless, such lessons from the past do not effectively inform our scenarios for either current extinction or recovery given the emphatic role of humans in both processes.

Near-Term Scenarios for Recovery: A Strategy

Given the limited applicability of the record of past extinction events for examining the current environmental crisis, it seems appropriate to turn to near-term recovery scenarios—namely, scenarios that relate to human intervention just as they flow from human causation. Such a consideration involves at least three steps. First, we must identify the threats to the biota and the entities most vulnerable to these threats. Second, we must consider the scientific principles or strategies that inform prescriptions to alleviate the threats. Third, we must apply feasible recovery strategies to aspects of the biota that are not filtered out during the transformation.

Any consideration of recovery also comes with an important provision. Recovery cannot be decoupled from preventative measures—namely, the environmental expression of "preventative medicine." In other words, any success in recovery is profoundly dependent on the state of what we have to work with. Many recovery measures have failed because of the utterly degraded and poorly understood state of the habitat at the time of remediation. At the very least, a proper consideration of the degree and nature of the threat and the scientific validity of a chosen remediation—namely, steps one and two—must be applied.

Our working group identified some primary current threats to biodiversity, which include: (*i*) pollution, (*ii*) over-harvesting, (*iii*) environmental shifts (climate change, disruption of biogeochemical cycles, etc.), (*iv*) introduced, invasive species (biotic exchange), (*v*) habitat loss and fragmentation through land use, and (*vi*) disruption of community structure in habitats.

This list bears some expected convergence on a set of drivers of change in terrestrial (excluding freshwater) ecosystems projected by Sala *et al.* (13) to have the greatest impact by the year 2100. These authors provide some predictions of change that depend on the degree of interaction of the drivers. The extent to which such global scale analyses frame a strategy for conservation priorities is likely to be a matter of debate for some time. What follows here is a consideration of the threats and the strategies for their mitigation that seem most grounded in credible scientific approaches.

Pollution. The environmental movement, inspired by Rachel Carson's (17) powerful disclosure of the deleterious impact of DDT and other pesticides, focused on the effects of toxins and other pollutants long before the more complex and subtle impacts of land use, biotic exchange, and climate change had been carefully considered. Nonetheless, recovery from environmental changes induced by pollution still faces severe problems in both analysis and action. During the last four decades, use of pesticides has tripled to 2.5 million metric tons of herbicides, fungicides, and insecticides each year, a massive load on the world's ecosystems represented by 50,000 different products (18). The deleterious effects of water-borne contaminants on both fresh water and marine ecosystems are well documented (19–22). Scientific analyses are critical to the ongoing effort to understand this chain of events and to improve guidelines for pollution control.

One danger addressed by such efforts is the mismatch between the scale of the effect and the cause. The devastation of the coral reefs, sea grasses, and kelps in the Caribbean has been promoted by the loss of benthic producers whose viable populations in turn may have been greatly reduced by pollutants in runoff released through human activity along the shoreline (8, 9). What may at first appear to be a complex crisis of subtle ecological dynamics could have a very direct and efficiently corrected cause—namely, the introduction of the pollutants in the first place. One constructive effort here is the continual refinement of categories of pollutants according to both the scale (global and local) and intensity (degree of toxicity, mutagenic impact, etc.) of the effects. This often requires exacting experimental work, as in the identification of a link between polyvinyl chlorides (PVCs) in packaging and carcinogenic chemicals (21). Such toxin detective work must be applied to a much broader range of potential cases.

Overharvesting. There is of course a clear and overlapping relationship between overharvesting and other threats to biodiversity, such as land use, but the matter deserves distinction here. Overharvesting impacts natural habitats with food sources that are less dominated by agriculture or other human activities that lead to transformation of the habitat.

Perhaps the most notable targets for overharvesting are freshwater and marine ecosystems. Intensive and indiscriminant fishing in freshwater systems, such as Lake Victoria in East Africa has demonstrable catastrophic impacts on biodiversity (23, 24). Likewise, Marine fisheries respond to food demand with catches often comprising large species, lopping off each summit of the food pyramid as populations of larger, top-level consumers are virtually eradicated (9). Humans harvest the equivalent of 24–35% of all diatom production in coastal and continental-shelve areas of the oceans via fish harvests (22, 25). Practices that minimize the effects of harvesting are often insufficiently grounded and weakly executed (26). Massive catches of species such as shrimp involve significant bycatches that are simply discarded.

There are success stories in constraining overfishing that should provide models for other practices. Strict management is resulting in recovery of summer flounder, mackerel in some areas, and most notably, striped bass (26). The apparent resurgence of lobster populations off the Maine coast clearly demonstrates the necessity of excluding large, gravid females as well as young from the catch and developing a surveillance for both the lobster fishing sites and the few points where catches are brought ashore for transport. A more analytical approach to constraining overharvesting also requires a revision in the standards and criteria for the haul. Most prescriptions for maximum sustainable yield (msy) concern only one species to the detriment of other species in the relevant food web. This selectivity disrupts ecologically sound practices that minimize the bycatch and preserve the balance of populations of interacting species. There is a clear need for better multispecies models and harvesting strategies.

Environmental Shifts: Climate Change and the Alteration of Global Biogeochemical Cycles. We continue to recognize the interplay between the transformation of the physical environment at three levels: hydrosphere, atmosphere, and lithosphere. As indicated by the current trends, the feedback among these three levels will intensify and the rate of change will accelerate. In recent years, two aspects of such shifts have received the most attention—climate change, involving both elevated carbon dioxide concentrations in the atmosphere and global warming, and nitrogen deposition.

Some suggest that the effects of climate change on the current biota are already observable in the terms of physiology, distribution, and phenology (27). For example, warming of the oceans could seriously impact on the convergence of warm water and cold water that is responsible for the nutrient-rich upwelling in the Southern Ocean off the coast of Antarctica. This change in current regimes could in turn reduce one of the sea's main staples: krill. These organisms account for about 250 million tons of food for whales, fish, seals, and other species annually, more than two and half times the annual yield of the world's fisheries (22).

The likelihood of unwelcome effects of climatic change presents a severe test for international science and environmental policy. The Kyoto Protocol, which sets specific targets for greenhouse gases for heavily industrialized nations—such as the reduction of CO_2 emissions by 5% of 1990 levels by 2008–2012—is an exemplary melding of scientifically based recommendations and policy; but it remains to be seen whether it will be widely ratified. Indeed, representatives of the Organization of Petroleum Exporting Countries (OPEC) are demanding financial compensation in the event that the goals of the Kyoto Protocol are realized and the demand for fuel oil decreases. As broad scale climatic change so emphatically transgresses regions, environments, and national boundaries, the success of recovery from detrimental effects of climatic change depends perhaps to a greater extent than any other measure on international coordination and cooperation.

A second major source of disruptions to the global environment is nitrogen deposition, ranked by Sala *et al.* (13) to be the third most influential driver of biodiversity change during the coming century. Human activity has essentially doubled the amount of nitrogen cycled globally (28), contributing to nitrogen sinks in soils, surface waters and deep oceans, and the atmosphere, and this increase has detrimental effects on biodiversity and ecosystem function.

Recovery efforts aimed at correcting the destructive aspects of nitrogen deposition often hinge on a simple recognition of the problem. Conservation actions to secure wildlife reserves rarely take into account the fact that nitrogen can negatively affect such reserves. Because nitrogen is transported globally through air and water, it can easily impact on areas and reserves that are seemingly in balance. Mitigation strategies must include anti-pollution efforts and control of fertilizer application. Because fertilizer is the greatest human source of additional nitrogen (28), there is a nascent effort to monitor and constrain its use. Studies of reduced nitrogen fertilizer use in Mexico (29) showed that crop yield and economics were sustained or even improved, while loss of nitrogen from the environment occurred at acceptably lower levels. More case studies of this kind are needed.

Introduced or Invasive Species. Biotic exchange is rampant and humans as agents are effective in all regions of the globe (30). Some of the more dramatic examples, such as the introduction of the Nile Perch into Lake Victoria and the resultant decimation of at least 200 endemic cichlids (23), offer sobering experiments that demonstrate the catastrophic effects of invasive species. Other introductions, such as plant species to the United Kingdom (31), do not seem to promote extinction of native plants because the invaders are restricted to habitats, such as roadsides and construction sites, that are highly disturbed by humans. Regardless of their magnitude, human-mediated introductions of species in new habitats and areas has and will continue to be one of the major drivers of biotic change (13, 32).

As biotic communities are widely infiltrated, it is critical to identify the degree of deleterious alteration by specific criteria. For example, it is difficult to generalize whether original habitats that are species-rich or species-poor are more or less susceptible to invasion. The probability and impact of biotic exchange is also closely tracked to other drivers, such as land use policy and introduction of excess nitrogen deposition through use of fertilizers. Accordingly, good policy to minimize biotic exchange must account for drivers that may promote an insidious and unintentional introduction of harmful species.

A key consideration in limiting biotic introductions, or at least their deleterious effects, relates to the nature of the maintenance of the ecosystem that is threatened by the introductions. Experiments conducted on patchy distributions, gene flow, and vagility of key community species (33) indicate a priority for preserving processes that maintain the balance within the community, not just the state described just before the onset of the invasion. Again, these strategies dovetail with land use and preservation policy. Fragmentation of habitats impedes the security of these processes because it restricts the movement and gene flow exchange of the resident, noninvasive organisms. On the other hand, the restoration of the historic disturbance regime, such as the reintroduction of fire in a community dependent on fire for seed germination or the removal of dams that prevent seasonal flooding necessary for establishment, has a way of reducing the invasive efforts and favoring the endemic components.

Habitat Loss and Fragmentation Through Land Use. Land use has been ranked as the most intensive driver of terrestrial environmental change in the coming century (13). Forecasted needs for world human populations over the next few decades will, if anything, accelerate massive demands on natural habitats. In 30 years there will be a need to feed an estimated 8.2 billion people, 32% more than exist today. To boost food production by the required 50 or 60%, grain harvest will have to increase by 2% a year, whereas agricultural breakthroughs have produced only 1.8% cumulative total growth for the 10 years between 1985 and 1995 (34). The harvesting required will have its own negative consequences; land use over the past two decades presents a disturbing picture of degradation. Over the past 20 years some 5 billion tons of topsoil have been removed and during the past 40 years at least 4.3 million square kilometers of cropland (more than twice the size of Alaska) have been abandoned because of soil loss. Each year, an estimated 13 million ha of tropical forests are destroyed, causing the loss of 14,000–40,000 species (35).

Projections for the impact of land use on the planet's biota are indeed so stark that any conservation effort seems engulfed by the tide of human activity. Yet there are scientifically grounded strategies and even some success stories in the effort to constrain the rampant destruction of natural habitats. One of these strategies applies criteria emphasizing marked biodiversity, high proportion of uniquely restricted (endemic) species, and vulnerability of ecosystems to a ranking of "biodiversity hotspots." Building on earlier proposals (1, 7), Myers *et al.* (36) identified 25 of the most obvious hotspots on continents and oceanic islands as high priority sites for intensive study and conservation effort. These designated crisis zones contain 44% of all species of vascular plants and 35% of all species in four vertebrate groups (mammals, birds, reptiles, and amphibians), yet they represent only 1.4% of the earth's surface.

Whether such a priority-based program for hotspot conservation is applied by governments or by international protocol, it is important to recognize one feature shared by many of these and other natural habitats: they are already in a marked state of degradation. Eleven of the 25 hotspots cited (36) have already lost 90% of their primary vegetation and three of these have lost 95%. Moreover, the average proportion of area currently protected for the total designated area of these hotspots is only 37.7%. Even areas that do receive a higher degree of "official protection" are highly vulnerable to threats from outside the system, including the climate change, pollution, nitrogen deposition, and species invasions noted above.

These observations underscore the need for realism and practicality, combined with solid scientific evidence, in any measures to minimize the impact of land use on biodiversity. We are obviously past any point where strategies that focus on preservation of "pristine" habitats are sufficient for the job. Greater attention must be placed on human-dominated landscapes that represent contours encircling the less disrupted areas. This is critical to identifying corridors or "landscape linkages" that facilitate the continuity among the less damaged habitats and help secure biological processes critical to functioning ecosystems (37). The approach is well exemplified in protocols established by Cowling *et al.* (38) for maintenance of viable ecological and evolutionary processes in the Cape Floristic Region, a remarkable area containing 12,000 plant species, 80% of which are endemic.

The size of either a "core area" or a "linkage area" is of course critical to securing biological process. It may be safely assumed that the bigger the area the more likely the processes will be maintainable and will require less recovery effort and intervention. Reality dictates, however, that the land secured for management will likely be smaller than the area desired. Therefore, high intensity scientific research on species identity, diversity, composition, distribution, trophic relationships, vagility, gene flow, and other patterns and processes must inform any decisions about the characteristics, including size, of the areas designated for conservation. Disclosures on species and their distributions for diverse organisms, including poorly known groups such as soil invertebrates, insects, bacteria, and fungi, can identify new critical areas of high endemism. Insights into ecological relationships build on such fundamental biodiversity information by providing some minimum expectations for core area or linkage area size. They specify a lower bound under which ecosystem processes will break down. Such work is critical to defining ecotones or ecological gradients that closely relate to the stability of the ecosystem in a given region. Such insights are necessary for developing practical and effective conservation strategies, especially where human populations and wildlife communities are so highly integrated.

Disruption of Community Structure in Habitats. The threat to the basic workings of community dynamics is, as noted above, broadly overlapping with other threats including land use. Yet this factor is distinguished here because ecological disruption is not only a manifestation of the reduction in size of the original habitat. Ecological havoc can occur in areas where, at least on the face of it, the original habitat has been "protected." Such putatively secured habitats may be vulnerable to many threats, such as population fragmentation of keystone species, disruption of biogeochemical cycles, or invasive species. One of the most disruptive factors to community stability is the interference with a balance of evolutionary processes, such as genetic drift and gene flow, that ensure genetic variation in species (33).

The importance of ecological relationships as a cornerstone to conservation of natural landscapes can be appreciated in the case of large-bodied species. Although information on the diversity and interactions in a great range of biological groups may be lacking for a given area, the need to secure relatively large areas for larger-bodied species is straightforward. As Western notes (37), maintaining this simple equation between area size and the protection of large-bodied species is important because the loss of the latter allow unwanted and significant changes to the ecological processes inherent in the community. Hence, the focus of conservation effort on some of the large, more charismatic species in major wildlife reserves is not only a matter of aesthetics or biophilia; it is critical to maintaining basic ecological relationships within the community.

Consideration of the roles of large-bodied species or other ecological functions in a community has pivotal importance in maintaining natural habitats, especially where a more complete picture of both the diversity and interactions within the community is still lacking. Such studies provide threshold values for securing core and linkage areas in both relatively isolated and human-dominated habitats. It is apparent that such parameters lead to conservation plans that can preserve not only the major components of diversity within an ecosystem, but the interactions that ensure the viability of the community as a whole. There are notable success stories based on this premise. Analysis of the breeding and migratory patterns of Chinook salmon (which can grow to 100 pounds as adults) in the State of Washington's Elwha River led to the recommendation to remove the two dams that inhibited the movement of the salmon upriver. The study showed that such an action would restore Chinook salmon populations to their former size—annually, about 400,000 adults. These recommendations inspired government action that would represent the most significant effort to reverse more than a century of dam building and help restore the nations rivers and their biodiversity (39).

Biodiversity Loss and Recovery Scenarios in Human-Dominated Ecosystems

Repeated throughout this discussion is the notion that the success of any restoration or recovery practice hinges on the state of what "we've caught in the net." Thus, vastly improved information on the basic state of the world biota and the various comparative states of degradation ongoing or projected remains a profoundly important goal for the conservation of biodiversity. The level of the challenge this goal presents can be appreciated when we consider the imbalance between urgency and investment. Patterns of species diversity and endemism critical to identifying hotspots or other conservation priorities are the products of work by experts in systematic biology—the science involving the identification, analysis of evolutionary relationships, and classification of diverse species and the groups that contain them. Only about 6,000 specialists (40) are responsible for organizing and updating the database on the 1.6 million named species, and potentially millions of more species yet to be discovered. Indeed, the cataloged species already represented by nearly 3 billion specimens in museums, botanical gardens, herbaria, frozen tissue collections, seed banks, bacteria type cultural collections, zoos, and aquaria are inadequately covered by the world's systematists (40, 41). The problem is especially acute when one considers that many of the countries that own hot spots and otherwise account for 80% of the world's named species have only about 6% of the world's scientists in any field. Building taxonomic and management capacity in these countries is essential to the success of conservation efforts. Such scientific investments that serve international conservation interests are meager compared with investments in space exploration (36).

It is well recognized, nonetheless, that the accumulation of scientific information itself is not the solution to our ecological problems. As we strive to improve our knowledge of biodiversity and ecological relationships we must also deal with perhaps the most subtle and complex community relationship within those ecosystems—the multifaceted roles of our own species. As Janzen (42) remarked, "The wildland garden is not humanity free and it never can be." The recognition that the planet is embraced by human-dominated ecosystems (37, 43) undercuts any assumption that we can restore the biota back to some state recognized as ideally pristine and "uncontaminated" by the mark of human populations. Human activity is as much, or more, a part of the ecological equation as any other factor. The problem of how human populations can adopt practices that are mutually beneficial to themselves as well as to the sustainable state of the biota remains. Some impractical hubris here should be avoided. There is little justification to convincing farmers that intensified monoculture is less productive and sustainable than the application of biodiversity extraction, because the latter is so limited relative to intensive farming (37, 44). Even successful conservation actions, such as the restoration effort of the Elwha River noted above (39), were spurred on by a shift in human needs and priorities—in this case an interest in larger salmon populations for food, sport, and ecotourism.

At a more general level, the most effective argument that human activities should safeguard biodiversity is the need to secure the basic ecosystem services dependent on that diversity. Ecosystem process and function effected by a critical number of interacting species secures the quality of the environment on the broadest front and, thus, has direct impact on human health and well-being (45). This is not an easy argument to make to highly competitive and heavily consuming populations in industrialized countries or to impoverished, marginalized populations in developing countries. But the argument, nonetheless, must be made, through demonstration of the services the natural world provides and the benefits of living compatibly with biodiversity.

In the world of uncertainty surrounding the nature of global biodiversity, the nature of its destruction, and the most effective steps for mitigating that destruction, scenarios for recovery are far from clear. Nonetheless, our review and discussion of many aspects treated in this colloquium do permit several general impressions and recommendations. Although major extinction events of the past underscore the reality and the possibility of such catastrophes today and in the future, they provide limited insight on the current biodiversity crisis. Such past extinction events do, however, suggest that if recovery is left to natural processes, the rebound of global ecosystems to some state beneficial to many of its species, including humans, is measured in unacceptably long timescales—on the order of millions or even tens of millions of years. Intervention on the part of the source of these current traumas, namely humans, is required for any possibility of recovery or even maintenance of the biota in any condition that approaches its present state.

Current efforts on this front suffer from several deficiencies, including a lack of basic information concerning the diversity and distribution of species, ecological processes, and relative magnitude of threats (land use change, pollution, nitrogen deposition, and others) in many habitats and regions. A much greater and more urgently applied investment to address these deficiencies is obviously warranted.

In addition, many plans for conservation and restoration in human-dominated ecosystems have not achieved sufficient connections between agricultural or harvesting practices and biological sciences. A number of threats to biodiversity require particularly intensive international cooperation and input from the scientific community to mitigate their harmful effects, including climate change and alteration of global biogeochemical cycles. The overarching recognition that we live in a world already radically transformed by human activity must frame our strategies for effecting maintenance or recovery of our vital ecosystems.

In addition to colloquium organizers Norman Myers and Andrew Knoll, we thank F. Bazzaz, D. Bramble, D. Erwin, J. Jackson, S. Kark, A. Templeton, D. Western, and others for their participation in the panel discussion.

1. Wilson, E. O. (1992) *The Diversity of Life* (Harvard Univ. Press, Cambridge, MA).
2. Myers, N. (1993) *Environ. Conserv.* **20,** 9–16.
3. Lawton, J. H. & May, R. M. (1995) *Extinction Rates* (Oxford Univ. Press, Oxford).
4. Pimm, S. L., Russel, G. J., Gittleman, J. L. & Brooks, T. M. (1995) *Science* **269,** 347–350.
5. Sepkoski, J. J., Jr. (1992) in *Systematics, Ecology and the Biodiversity Crisis*, ed. Eldredge, N. (Columbia Univ. Press, New York), pp. 77–100.
6. Erwin, D. H. (1993) *The Great Paleozoic Crisis* (Columbia Univ. Press. New York).
7. Myers, N. (1988) *The Environmentalist* **8,** 187–208.
8. Knowlton, N. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5419–5425.
9. Jackson, J. B. C. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5411–5418.
10. Kirchner, J. W. & Weil, A. (2000) *Nature (London)* **404,** 177–180.
11. Jablonski, D. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5393–5398.
12. Erwin, D. H. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5399–5403.
13. Sala, O. E., Chapin, F. S., III, Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Henneke, L. F., Jackson, R. B., Kinzig, A., *et al.* (2000) *Science* **287,** 1770–1774.
14. Archibald, J. D. (1996) *Dinosaur Extinction and the End of an Era: What the Fossils Say* (Columbia Univ. Press, New York).
15. Novacek, M. J. (1999) *Ann. Mo. Bot. Gard*. **86,** 230–258.
16. Hoffmann, H. J. (2000) *Nat. Geo.* **198,** 100–113.
17. Carson, R. (1962) *Silent Spring* (Houghton Mifflin, Boston).
18. Catley, K. M. (2001) in *The Biodiversity Crisis. Losing What Counts*, ed. Novacek, M. J. (Amer. Mus. Nat. Hist./The New Press, New York), pp. 100–104.
19. Fowler, S. W. (1990) *Mar. Environ. Res.* **29,** 1–64.
20. Anderson, D. M. (1994) *Sci. Am.* **271,** (August) 62–68.
21. Culborn, T., Dumanoski, D. & Myers, J. P. (1996) *Our Stolen Future* (Dutton/Penguin Putnam, New York).
22. Myers, N. (1997) *Environ. Dev. Econ.* **2,** 88–93.
23. Witte, R., Goldschmide, T., Wanink, J., Van Oijen, M., Goudswaard, K., Witte Maas, E. & Bouton, N. (1992) *Environ. Biol. Fishes* **34,** 1–28.
24. Stiassny, M. L. J. (2000) in *The Biodiversity Crisis: Losing What Counts*, ed. Novacek, M. J. (Amer. Mus. Nat. Hist./The New Press, New York), pp. 116–119.
25. Pauley, D. & Christensen, V. (1995) *Nature (London)* **374,** 255–257.
26. Safina, C. (1998) *Audubon Magazine* **100,** 64–66.
27. Hughes, L. (2000) *TREE [Rep.]* **15,** 56–61.
28. Vitousek, P. M., Aber, J. D., Howarth, R. W., Likens, G. E., Matson, P. A., Schindler, D. W., Schlesinger, W. H. & Tilman, D. G. (1997) *Ecol. Appl.* **793,** 737–750.
29. Matson, P. A., Naylor, R. & Monasterio, I. O. (1998) *Science* **280,** 112–115.
30. Vitousek, P. M., D'Antonio, C. M., Loope, L. L. & Westbrooks, R. (1996) *Am. Sci.* **84,** 468–478.
31. Crawley, M. J. (1987) in *Colonization, Succession, and Stability*, eds. Gray, A. J., Crawley, M. J. & Edwards, P. J. (Blackwell Scientific Publications, Oxford), pp. 429–453.
32. Mooney, H. A. & Cleland, E. E. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5446–5451.
33. Templeton, A. R., Robertson, R. J., Brisson, J. & Strasburg, J. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5426–5432.
34. Myers, N. (1998) in *Food Security: New Solutions for the 21st Century*, ed. Johnson, S. R. (Iowa State Univ. Press, Ames), pp. 185–220.
35. Food and Agricultural Organization (1999) *State of the World's Forests* (FAO, Rome).
36. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonsca, G. A. B. & Kent, J. (2000) *Nature (London)* **403,** 853–858.
37. Western, D. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5458–5465.
38. Cowling, R. M. & Pressey, R. L. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5452–5457.
39. Thomas, J. (2000) in *The Biodiversity Crisis: Losing What Counts*, ed. Novacek, M. J. (Am. Mus. Nat. Hist./The New Press, New York), pp. 189–190.
40. Wilson, E. O. (2000) *Science* **289,** 2279.
41. Cracraft, J. (2001) in *The Biodiversity Crisis: Losing What Counts*, ed., Novacek, M. J. (Amer. Mus. Nat. Hist./The New Press, New York), pp. 150–154.
42. Janzen, D. H. (1998) in *Nature and Human Society: The Quest for a Sustainable World*, eds. Raven, P. R. & Williams, T. (Natl. Acad. Press, Washington, DC).
43. Rosenzweig, M. L. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5404–5410.
44. Browder, J. O. (1991) *Bioscience* **41,** 286.
45. Daily, G. C., ed. (1997) *Nature's Services: Societal Dependence on Natural Ecosystems* (Island Press, Washington, DC).