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INTRODUCTION

COLLOQUIUM PAPERS

The biotic crisis and the future of evolution

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The biotic crisis overtaking our planet is likely to precipitate a major extinction of species. That much is well known. Not so well known but probably more significant in the long term is that the crisis will surely disrupt and deplete certain basic processes of evolution, with consequences likely to persist for millions of years. Distinctive features of future evolution could include a homogenization of biotas, a proliferation of opportunistic species, a pest-and-weed ecology, an outburst of speciation among taxa that prosper in human-dominated ecosystems, a decline of biodisparity, an end to the speciation of large vertebrates, the depletion of "evolutionary powerhouses" in the tropics, and unpredictable emergent novelties. Despite this likelihood, we have only a rudimentary understanding of how we are altering the evolutionary future. As a result of our ignorance, conservation policies fail to reflect long-term evolutionary aspects of biodiversity loss.

Human activities have brought the Earth to the brink of biotic crisis. Many biologists (e.g., refs. 1–5) consider that coming decades will see the loss of large numbers of species. Fewer scientists—witness the lack of professional papers addressing the issue—appear to have recognized that, in the longer term, these extinctions will alter not only biological diversity but also the evolutionary processes by which diversity is generated. Thus, current and predicted environmental perturbations form a double-edged sword that will slice into both the legacy and future of evolution.

A simple consideration of time underscores the magnitude of the challenge to scientists and public alike (*cf.* ref. 6). Episodes of mass extinction documented in the geological record were followed by protracted intervals of rediversification and ecological reorganization; five million years can be considered a broadly representative recovery time, although durations varied from one extinction to another (7). Suppose, too, that the average number of people on Earth during the recovery period is 2.5 billion (by contrast with the 6 billion today). Under these conditions, the total number of people affected by what we do (or do not do) during the next few decades will be in the order of 500 trillion—10,000 times more people than have existed until now. We are thus engaged in by far the largest "decision" ever taken by one human community on the unconsulted behalf of future societies.

The question of how current threats to biological diversity will affect the future of evolution was first raised by one of us in the mid-1980s (8). It attracted virtually zero interest from fellow biologists. Thirteen years later, he revisited the question, this time with more detailed analysis, although still in exploratory form (9). This latter publication elicited attention from the National Academy of Sciences, which undertook to sponsor a Colloquium in March 2000. As a "scene setter" for Colloquium participants, we drafted an overview account of topics to be tackled, and that draft makes up the bulk of this paper. We hope that it may serve the same purpose for readers of this special section of PNAS.

The Core Concept

One of the first truisms absorbed by biologists is that evolution is not predictable. We can no more predict the future composition of communities than some Ordovician ecologist could have foreseen the Great Barrier Reef. However, despite our inability to predict the *products* of evolution—the trajectories of future morphologies or the innovations of future physiologies—we *can* make meaningful estimates about evolutionary *processes* as they will be affected by the depletion of biological diversity. We may have little basis for predicting what large mammals might look like two million years from now, but much better reason to suppose that there will be very few of them.

The evolutionary dimension to the current biotic crisis has been vividly expressed by Michael Soule (10): "Death is one thing, an end to birth is something else." In other words, impending extinctions will be far from the full final outcome of current environmental disruption. At least as important will be the alteration of evolutionary process, and for a period that is difficult to estimate but must surely measure in millions of years.

First-Order Effects. There will be several first-order effects stemming from the biotic crisis: (*i*) a major extinction of species within the foreseeable future, estimated by some to remove between one-third and two-thirds of all species now extant (1, 2, 5, 11); (*ii*) a mega-mass extinction of populations, proportionately greater than the mass extinction of species, within the foreseeable future (12); (*iii*) alien invasions and other mixings of biotas (13–16); (*iv*) progressive depletion and homogenization of biotas, with potential threshold effects on ecosystems (17, 18); (*v*) biotic impoverishment generally, possibly including a decline of global biomass (18–20); and (*vi*) gross reduction if not virtual elimination of entire sectors of some biomes, notably tropical forests, coral reefs, and wetlands, all of which have served as centers of diversification in the past (21–24).

Further Evolutionary Effects. These first-order impacts will likely engender a series of further consequences, including although not limited to: (*i*) fragmentation of species' ranges, with disruption of gene flow (25–28); (*ii*) decline in effective population sizes, with depletion of gene reservoirs/pools (12, 29, 30); and (*iii*) biotic interchanges introducing species and even biotas into new areas, with multiple founder effects and novel competitive and other ecological interactions (13, 16, 31). These impacts, in turn, might disrupt food chains/webs, symbioses, or other biological associations (32, 33).

These consequences could lead to further repercussions such as the following six:

An outburst of speciation. As large numbers of niches are vacated, in conjunction with a splitting off of disjunct populations through habitat fragmentation, there may well be an outburst of speciation, even of adaptive radiation, albeit not remotely on a scale to match the extinction spasm (34–36). It is unlikely that speciation will be evenly distributed among surviving lineages; it may be concentrated among particular clades or

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ecological types that thrive in human-dominated ecosystems (37, 38)?

Proliferation of opportunistic species. r-selected and generalist species, often appearing as opportunistic species, may proliferate, especially if there is preferential elimination of K-selected species that include natural controls of r-selected populations (32, 38). Could this proliferation lead to what has been characterized as a "pest and weed" ecology (39, 40)?

Depletion of "evolutionary powerhouses" in the tropics. Virtually every major group of vertebrates and many large categories of invertebrates and plants originated in spacious zones with warm, equable climates (41, 42). In addition, tropical species appear to have persisted for relatively brief periods of geologic time, implying high rates of evolutionary turnover and episodes of explosive speciation (21, 43, 44). According to Jablonski (22), the tropics have been "the engine of biodiversity" for at least 250 million years. Today, we face the prospect of severe depletion if not virtual elimination of tropical forests, wetlands, estuaries, coral reefs, and other biomes, with their exceptional biodiversity and ecological complexity. Because some of these biomes appear, in some senses at least, to have served in the past as preeminent "powerhouses" of evolution (45, 46), their decline could entail severe consequences for rediversification as the biosphere emerges from environmental crisis.

Decline of biodisparity. Elimination of species is not the only measure of an extinction event. There can be declines, as well, in biodisparity, the biota's manifest morphological and physiological variety (47–49). Biodisparity impoverishment can be assessed through the surrogate measure of loss of higher taxa or guilds, and, over the past 2000 years, the preferential elimination of species-poor genera has reduced biodisparity at rates even greater than those of species loss (48). Will the same pattern of non-random culling persist in the future?

An end to speciation of large vertebrates. Even our largest protected areas will prove far too small for further speciation of elephants, rhinoceroses, apes, bears, and big cats, among other large vertebrates (30, 50, 51). What knock-on consequences and ripple effects could there be for smaller species, indeed for biotas as a whole given, for example, the depauperizing impacts of the present-day decline of elephants (52)?

Emergent novelties. There may be many emergent novelties, although these are especially difficult to predict. For instance, there could be an explosive radiation within certain higher taxa, notably small mammals and insects able to thrive in human-dominated ecosystems. The question is not whether persistent lineages can evolve in unexpected ways, but rather to what extent the environmental constraints humans place on surviving populations will channel innovations toward properties we associate with pests.

Lessons from the Past?

The geological record is replete with extinction events, their intensity ranging from the small and local to global mass extinctions that shattered Earth's biological order. Inevitably, extinctions were followed by rediversification, directed in the case of the largest events by ecological reorganization. What can we learn from paleobiology, other than the oft-quoted observation that recovery proceeds slowly in the wake of grand scale biotic disruption (40, 53, 54)? Can we find generalities among extinction episodes that can guide thinking about our own future? Or, is it the differences among extinction events that should command our attention? As David Jablonski (63) asks in these proceedings, should we even focus on the five great mass extinctions that capture most attention, or do the more numerous, smaller events scattered throughout the geological record provide closer analogs for the present?

The geologic record contains much evidence of bounce-back processes (49, 54–59), but how far will these serve as analytic blueprints for what lies ahead? How can we estimate time frames at issue? Should we anticipate a minimum period of several million years [perhaps as much as 10 million (56)] before evolution can reestablish anywhere near the biological configurations and ecological circuitry existing before the current crisis? Will some recovery processes operate in some sectors of the biosphere, others in others, and with widely varying rates (55, 58, 60)?

In some major extinctions, for example the Cretaceous-Tertiary boundary event, environmental perturbation was swift and sure, but also short-lived. Recovery began soon after disruption. In the present biotic crisis, it is hard to envision a scenario under which the factors that are driving the biosphere toward grand scale biodiversity loss will be mitigated in the wake of such loss. On the contrary, on any time scale we can envisage (and any scenario that does not involve early mass mortality for humankind), the situation becomes bad and then stays bad for some time to come. Thus, on the time scale of the human species, environmental disruption (or at least aspects of it) is permanent. Under these circumstances (which may, to some degree, be approximated by the persistent environmental discord after the Permian-Triassic mass extinction), the prospects for rediversification are limited.

Recovery Processes

How will ecosystems function in a world of diminished biodiversity? Does ecosystem function necessarily decay as diversity declines, and if so, by how much and in what manner? Can biodiversity and humans alike prosper in a world where most biological diversity will be confined to relatively small parks and reserves?

If biodiversity is indeed critical to ecosystem function, do we know enough about the principles of evolution to intervene in the recovery processes? To the extent that the answer to the first part of this question is probably "yes" and the answer to the second part is almost certainly "no," what would we need to learn to attempt evolutionary interventions that will do more good than harm?

More realistically, do we know enough to mitigate the loss of biological diversity? As David Western writes in his colloquium contribution, mitigating strategies will likely be carried out predominantly in ecosystems dominated or influenced by humans and other species that thrive when humans are present. How we think about our evolutionary future depends directly on how successful we can hope to be in preserving biodiversity and biodisparity.

Which taxa are likely to play prominent parts in recovery processes? What "survivorship" traits (ecological, biogeographic, evolutionary) can we use to define those taxa that may prove more successful in surviving current events? At the same time, which taxa might [to cite Erwin's graphic phrase (55)] "win the extinction but lose the recovery?" Might certain biotas already be "stressed" by Pleistocene climatic oscillations, making them more vulnerable to depletion (61, 62)? Or are they "hardened"—purged of their most vulnerable members by Pleistocene events (63)?

Should we in fact speak of "recovery"? What is it that is supposed to be recovering (the dinosaurs didn't)? Should we not view the recovery phase as more like a transition to new and novel departures of multiple sorts (55)? Plainly there is much scope for pioneering research in response to the many questions raised (54). We need to consider planning priorities. What research is most pressing? What is readily achievable? What is already underway? What deserves most financial or institutional support? What potential is there for interdisciplinary research, for instance that which combines genetics and restoration ecology, or paleontology and conservation biology?

Conservation Responses

Should we be content simply to safeguard as much as we can of the planetary stock of species? Or should we pay equal if not greater attention to safeguarding evolutionary processes at risk (cf. refs. 64–66)? Consider, for instance, biodisparity: to cite Jablonski (49), "If we are concerned with avoiding the loss of particular functional groups, or with maximizing the potential source pool for evolutionary recovery, then biodisparity measures may provide a more appropriate assessment, beyond sheer numbers of taxa, of how priorities should be set."

Following on from these considerations is the question of whether we should seek to maintain the evolutionary status quo by preserving precise phenotypes of particular species, or whether we should prefer to maintain phylogenetic lines that will enable evolutionary adaptations to persist, thereby leading to new species (67, 68). Is it sufficient for us to maintain, for example, just the two elephant species we already have, or should we try to keep open the evolutionary option of further elephant-like species in the distant future?

This is an unusually significant question, with unusually significant implications for conservation strategies. Elephants, along with many other large mammals, are inclined to move around a good deal, a trait that enables them to maintain gene flow across large areas. As a result, their gene pools often tend to be fairly uniform [an elephant in East Africa may not be so different from one 4,000 km away in South Africa (68)]. Regrettably the remaining populations of elephants, substantial and extensive as they are, albeit fragmented and declining fast, are probably already below the minimum numbers to keep open the possibility of speciation (69).

In marked contrast to elephants, with their slow breeding rates, many insect species have immense breeding capacities and rapid turnover rates. These latter attributes offer quick adaptability to environmental shifts, whereupon genetic changes are passed along promptly. These attributes not only leave many insect species well suited to survive the environmental upheavals of human activities, but they offer exceptional scope for speciation in comparatively short order. By contrast, elephants, together with other large-bodied species that reproduce slowly and hence possess restricted capacity for genetic adaptation, will be at an extreme evolutionary disadvantage. Does this factor imply that they should therefore receive all of the greater attention from conservationists—or that, in a triage situation, they should rank lower in our priorities? Although this is a fundamental question, it has hardly been addressed.

An even more important consideration arises concerning those origination centers and radiation lineages that serve as "evolutionary fronts" (67). From the standpoint of future evolution, it is surely more appropriate to safeguard the main potential for diversity generation than to emphasize the primary focus of many current conservation programs, viz. individual taxa and, especially, endemic taxa (70, 71). Much the same applies with respect to those functional groups that increase the potential for evolutionary recovery (49).

All in all, the prospect is that, in the wake of the present biodiversity crisis, we shall find that many evolutionary processes that have persisted throughout the Phanerozoic Eon will be slowed if not depauperized for an extended period. This is not to say, of course, that evolution will come to a halt, or even that speciation will be suspended (except for the large vertebrates). In fact, there may be enough creative disruption in certain environments to foster some extremely rapid microevolutionary changes, attended by (localized?) bursts of speciation. But there will surely be reduced scope for speciation on the scale that has characterized the past many millions of years.

These, then, are some of the issues that we should bear in mind as we begin to impose a fundamental shift on evolution's course. We are "deciding" on evolution's future in virtually a scientific vacuum—deciding all too unwittingly, but effectively and increasingly. Hence the importance of the Colloquium's findings as set out in this special issue of PNAS.

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1. Ehrlich, P. R. & Wilson, E. O. (1991) *Science* **253,** 758–762.
2. Myers, N. (1993) *Biodiversity and Conserv.* **2,** 2–17.
3. Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. (1995) *Science* **269,** 347–354.
4. Raven, P. H. (1999) *Plants in Peril: What Should We Do?* (Missouri Botanical Garden, St. Louis, MO).
5. Wilson, E. O. (1992) *The Diversity of Life* (Harvard Univ. Press, Cambridge, MA).
6. Ehrlich, P. R. (2000) *Human Natures: Genes, Cultures and the Human Prospect* (Island Press, Washington, DC).
7. Erwin, D. H. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5399–5403.
8. Myers, N. (1985) *Nat. Hist.* **94,** 2, 6, 12.
9. Myers, N. (1996) *Environmentalist* **16,** 37–47.
10. Soule, M. E. (1980) in *Conservation Biology: An Evolutionary-Ecological Perspective*, eds. Soule, M.E. & Wilcox, B.A. (Sinauer, Sunderland, MA), pp. 151–170.
11. Pimm, S. & Raven, P. (2000) *Nature (London)* **403,** 843–845.
12. Hughes, J. B., Daily, G. C. & Ehrlich, P. R. (1997) *Science* **278,** 689–692.
13. Drake, J. A., Mooney, H. A., diCastri, F., Groves, R., Kruger, F., Rejmanek, M. & Williamson, M., eds. (1989) *Biological Invasions: A Global Perspective.* (Wiley, New York).
14. Mooney, H. A. & Hobbs, R. J., eds. (2000) *Invasive Species in a Changing World* (Island Press, Washington, DC).
15. Vermeij, G. J. (1991) *Science* **253,** 1099–1103.
16. Mooney, H. A. & Cleland, E. E. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5446–5451.
17. Walliser, O. (1995) *Global Events and Event Stratigraphy* (Springer, New York).
18. Woodwell, G. M., ed. (1990) *The Earth in Transition: Patterns and Processes of Biotic Impoverishment* (Cambridge Univ. Press, Cambridge, U.K.).
19. Hsu, K. J. (1989) *Hist. Biol.* **2,** 1–4.
20. McLaren, D. J. (1989) *Hist. Biol.* **2,** 5–15.
21. Briggs, J. C. (1996) *Conserv. Biol.* **10,** 713–718.
22. Jablonski, D. (1993) *Nature (London)* **364,** 142–144.
23. Raup, D. M. (1991) *Extinction: Bad Genes or Bad Luck?* (Norton, New York).
24. Knowlton, N. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5419–5425.
25. Kruess, A. & Tscharntke, T. (1994) *Science* **264,** 1581–1584.
26. Robinson, G. R., Holt, R. D., Gaines, M. S., Hambourg, S. P., Johnson, M. L., Fitch, H. S. & Martinko, E. A. (1992) *Science* **257,** 524–526.
27. Shorrocks, B. & Swingland, I. R., eds. (1990) *Living in a Patchy Environment* (Oxford Univ. Press, Oxford).
28. Templeton, A. R., Robertson, R. J., Brisson, J. & Strasburg, J. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5426–5432.
29. Avise, J. (1998) *The Genetic Gods* (Harvard Univ. Press, Cambridge, MA).
30. Lynch, M. & Lande, R. (1998) *Animal Conserv.* **1,** 70–72.
31. Mooney, H. A. & Drake, J. A., eds. (1986*) Ecology of Ecological Invasions of North America and Hawaii* (Springer, New York).
32. Pimm, S. L. (1991) *The Balance of Nature: Ecological Issues in the Conservation of Species and Communities* (Univ. Chicago Press, Chicago).
33. Schultze, E. D. & Mooney, H. A., eds. (1994) *Biodiversity and Ecosystem Function* (Springer, New York).
34. Benton, M. J. (1995) *Science* **268,** 52–58.
35. Feduccia, A. (1995) *Science* **267,** 637–638.
36. Nitecki, M. H., ed. (1990) *Evolutionary Innovations* (Univ. Chicago Press, Chicago).
37. Hoffman, A. A. & Hercus, M. J. (2000) *BioScience* **50,** 217–226.
38. Rosenzweig, M. L. (1995) *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, U.K.).
39. Gould, F. (1991) *Am. Sci.* **79,** 496–507.
40. Jablonski, D. W. (1991) *Science* **253,** 754–757.
41. Darlington, P. J. (1957) *Zoo Geography: The Geographical Distribution of Animals* (Wiley, New York).
42. Mayr, E. (1982) *The Growth of Biological Thought: Diversity, Evolution and Inheritance* (Harvard Univ. Press, Cambridge, MA).
43. Gentry, A. H. & Dodson, C. (1987) *Ann. Missouri Bot. Garden* **74,** 205–233.
44. Rohde, K. (1992) *Oikos* **65,** 514–527.
45. Jablonski, D. & Bottjer, D. J. (1990) in *Causes of Evolution: A Paleontological Perspective*, eds. Ross, R. M. & Allmon, W. D. (Univ. Chicago Press, Chicago), pp. 21–75.

46. Roy, K., Jablonski, D. & Valentine, J. W. (1994) *Proc. Natl. Acad. Sci. USA* **91,** 8871–8874.
47. Runnegar, B. (1987) in *Rates of Evolution,* ed. Campbell, K. S. W. & Day, M. F. (Allen and Unwin, London), pp. 39–60.
48. Russell, G. J., Brooks, T. M., McKinney, M. L. & Anderson, C. G. (1995) *Decreased Taxonomic Selectivity in the Future Extinction Crisis.* (Univ. Tennessee Press, Knoxville, TN).
49. Jablonski, D. (1995) in *Extinction Rates*, eds. Lawton, J. H. & May, R. M. (Oxford Univ. Press, Oxford), pp. 25–44.
50. Franklin, I. R. & Frankham, R. (1998) *Animal Conserv.* **1,** 69–70.
51. Soule, M. E. (1996) *World Conserv.* (IUCN) April, pp. 24–25.
52. Owen-Smith, N. (1998) *Megaherbivoires: The Influence of Very Large Body Size on Ecology*. (Cambridge Univ. Press, Cambridge, U.K.).
53. Raup, D. M. (1994) *Proc. Natl. Acad. Sci. USA* **91,** 6758–6763.
54. Sepkoski, J. J. (1997) *J. Paleontol.* **71,** 533–539.
55. Erwin, D. H. (1998) *Science* **279,** 1324–1325.
56. Erwin, D. (2000) *Nature (London)* **404,** 129–130.
57. Hallam, A. & Wignall, P. B. (1997) *Mass Extinctions and Their Aftermath* (Oxford Univ. Press, Oxford).
58. Jablonski, D. (1999) *Science* **284,** 2114–2116.
59. Raup, D. M. (1994) *Proc. Natl. Acad. Sci. USA* **91,** 6758–6763.
60. Kirschner, J. W. & Weil, A. (2000) *Nature (London)* **404,** 177–180.
61. Kauffman, E. G. & Walliser, O. H., eds. (1990) *Extinction Events in Earth History* (Springer, New York).
62. Martin, P. S. & Klein, R. G., eds. (1984) *Quaternary Extinctions: A Prehistoric Revolution*. (Univ. Arizona Press, Tucson, AZ).
63. Jablonski, D. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5393–5398.
64. Brooks, D. R., Mayden, R. L. & McLennan, D. A. (1992) *Trends Ecol. Evol.* **7,** 55–59.
65. Thompson, J. N. (1996) *Trends Ecol. Evol.* **11,** 300–303.
66. Thompson, J. N. (1998) *Trends Ecol. Evol.* **13,** 329–332.
67. Erwin, T. L. (1991) *Science* **253,** 750–752.
68. Franklin, I. R. (1980) in *Conservation Biology: An Evolutionary-Ecological Perspective*, eds. Soule, M. E. & Wilcox, B. A. (Sinauer, Sunderland, MA), pp. 135–149.
69. Georgiadis, N., Bischof, L., Templeton, A., Patton, J., Karesh, W. & Western, D. (1994) *J. Heredity* **85,** 100–104.
70. Erwin, D. H. (1994) *Nature (London)* **367,** 231–236.
71. Taylor, P. D. & Larwood, P. G. (1990) *Major Evolutionary Radiations* (Clarendon Press, Oxford, U.K.).

Lessons from the past: Evolutionary impacts of mass extinctions

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Mass extinctions have played many evolutionary roles, involving differential survivorship or selectivity of taxa and traits, the disruption or preservation of evolutionary trends and ecosystem organization, and the promotion of taxonomic and morphological diversifications—often along unexpected trajectories—after the destruction or marginalization of once-dominant clades. The fossil record suggests that survivorship during mass extinctions is not strictly random, but it often fails to coincide with factors promoting survival during times of low extinction intensity. Although of very serious concern, present-day extinctions have not yet achieved the intensities seen in the Big Five mass extinctions of the geologic past, which each removed ≥50% of the subset of relatively abundant marine invertebrate genera. The best comparisons for predictive purposes therefore will involve factors such as differential extinction intensities among regions, clades, and functional groups, rules governing postextinction biotic interchanges and evolutionary dynamics, and analyses of the factors that cause taxa and evolutionary trends to continue unabated, to suffer setbacks but resume along the same trajectory, to survive only to fall into a marginal role or disappear ("dead clade walking"), or to undergo a burst of diversification. These issues need to be addressed in a spatially explicit framework, because the fossil record suggests regional differences in postextinction diversification dynamics and biotic interchanges. Postextinction diversifications lag far behind the initial taxonomic and morphological impoverishment and homogenization; they do not simply reoccupy vacated adaptive peaks, but explore opportunities as opened and constrained by intrinsic biotic factors and the ecological and evolutionary context of the radiation.

To the conservation biologist, there is little positive to be said about extinction. From an evolutionary perspective, however, extinction is a double-edged sword. By definition, extinction terminates lineages and thus removes unique genetic variation and adaptations. But over geological time scales, it can reshape the evolutionary landscape in more creative ways, via the differential survivorship of lineages and the evolutionary opportunities afforded by the demise of dominant groups and the postextinction sorting of survivors. The interplay between the destructive and generative aspects of extinction, and the very different time scales over which they appear to operate, remains a crucial but poorly understood component of the evolutionary process.

The fossil record is rich in extinction events at all intensities and spatial scales, and thus provides the essential raw material for an extremely important research objective: the comparative calibration of evolutionary responses, both positive and negative, to perturbation. Despite limits on direct comparisons to present-day and future events, discussed below, paleontological data afford the opportunity to test the evolutionary impact of such factors as the initial state of the system, the nature, duration, and magnitude of the perturbation, and postextinction physical and biotic conditions. Comparative analysis of the Big Five mass extinctions (1, 2) is just beginning, as is work on the myriad smaller—and sometimes more localized—events manifest in the geologic record, and so this paper is as much a research agenda as a review. One approach to the problem is through the related issues of extinction selectivity and evolutionary continuity across mass extinction events in the geologic past. Recent work on the geographic fabric of extinction events and their aftermath suggests that the spatial dimension of diversity dynamics also will be an important component of a rigorous theory of extinction and its evolutionary consequences, and so although data are sparse I will raise some of these issues as well.

Selectivity and Loss

Mass extinctions would be important evolutionary agents even if they simply intensified variations in clade survivorship seen in times of low extinction rates. For example, if mass extinctions primarily removed lineages in decline or in the early stages of diversification, truncating the time span available to those and other clades for the acquisition of evolutionary novelties, then they would significantly reinforce the stability of the status quo. The fossil record shows, however, that the major extinction events of the geologic past have played a larger and more complex role, by removing not just marginal players but also dominant incumbents, owing at least in part to extinction selectivities that are partly independent of those seen under "normal" extinction regimes. For example, factors such as local abundance, species richness, and species-level geographic ranges, all apparently significant during times of low extinction intensities (3), played little role in the survival of marine invertebrate clades during the end-Cretaceous (K-T) mass extinction, where the data are most extensive (2, 4, 5, †), and have been unimportant in at least some of the other mass extinction events as well (2, 6). At the same time, broad geographic distribution at the clade level, regardless of species-level ranges, significantly enhanced survivorship at all of the major extinction events (2, 4, 7) (note that this discordance across hierarchical levels means that surviving clades need not consist of generalized or opportunistic species, contrary to some oversimplifications of these results). These analyses suggest that clades or adaptations may be lost not because they are poorly adapted to the pre(or post) disturbance settings, but because they lack the broad geographic deployment or other traits that favor survival during the extinction bottleneck—a pattern of "nonconstructive selectivity" (8) that yields differential survival among clades without promoting the long-term adaptation of the biota (2, 6, 9).

This is not to say that traits favored under low extinction intensities were never advantageous during mass extinctions: resting stages in phytoplankton, occupation of unperturbed

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Abbreviation: K-T, end-Cretaceous.

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habitats or regions, physiological tolerances that happened to match the extinction-driving stresses, and perhaps particular ecological strategies, all might play a role in survivorship (10–12). Further, the broad correspondence between survivorship during mass extinction and long-term clade volatility (variance in standing diversity, i.e., net diversification rates rather than per-taxon origination or extinction rate) (13–15) suggest that other intrinsic biotic factors (6) carry over from low to high extinction-intensity regimes. Little has been done to explore this possibility, however, or the alternative that taxa with high per-taxon turnover rates have a lower threshold for crossing into the mass-extinction selectivity regime.

Given that some clades show consistently severe or mild responses to extinction events, which suggests that intrinsic biotic factors are important determinants of survivorship, why does the vulnerability of other clades appear to vary significantly among extinction events (6, 16)? This question bears critically on the evolutionary consequences of extinction events but has received little attention. Potential explanations range from long-term hardening of clades by the removal—and failure to re-evolve—extinction-prone constituents, to contrasting forcing mechanisms in the different extinction events, to fortuitous trait combinations evolved under "background" extinction regimes. Such analyses also are needed to make better biological sense out of apparent selectivity against major clades (e.g., ammonites, mosasaurs, dinosaurs etc. at the K-T boundary) when other selectivities appear indifferent to clade membership [e.g., widespread vs. restricted-range bivalves and other taxa at many extinction events (2, 4)].

I should note that the terms background and mass extinction should be used carefully: major extinction events stand out in geologic time series as maxima against a local background of lower rates, but the overall frequency distribution of extinction intensities is a highly skewed, unimodal continuum (9). Contrasts in selectivity between the major extinction events and times of relatively low extinction suggest a threshold effect (2, 5), but the position and taxonomic generality of that threshold is uncertain; comparative analyses that encompass smaller extinction episodes such as the Cenomanian-Turonian and Eocene-Oligocene events would be valuable.

The likelihood of clade- or ecosystem-specific thresholds for the onset of mass-extinction selectivities underscores the complexity underlying extinction time series in the fossil record, a point sometimes lost in the general focus on a few of the most massive events. The direct comparability of the Big Five mass extinctions to present-day biodiversity losses remains unclear. Although present-day losses are severe and appear to be accelerating (17), they have yet to approach the scale of the Big Five extinctions of the geologic past. For example, the K-T extinction removed 50% of the marine bivalve genera globally (4), and 97% of the photosymbiont-bearing coral species (and 83% of those genera) (18), and the sampling biases inherent to the fossil record virtually require that these victims were drawn from the more abundant and widespread components of the biota (2, 9). Viewed in this light, these are shocking statistics that exceed even the most severe estimates for present-day losses, although long-term projections eventually can approach such magnitudes. Further, over the past 2,000 yr species-poor clades and geographically restricted species have been the overwhelming majority of losses (19), corresponding to an intense version of the "background extinction" regime rather than the mass extinction selectivities of the fossil record.

This is neither to belittle the violence being wrought on today's biodiversity, nor to imply that the fossil record offers few insights regarding the future of evolution in the face of human activities and other stresses. It does suggest, however, that the most useful comparisons must go beyond absolute extinction intensities to involve such factors as: relative extinction intensities among regions, clades and functional groups; long-term effects of geographic variation not only in extinction but also in postextinction biotic interchanges and evolutionary dynamics; patterns of biotic continuity, lag times, and innovation as reflected in postextinction evolutionary rates and patterns. Also important, of course, are the looming questions of what causes the transition to selectivities seen under paleontological mass-extinction regimes, and whether that threshold can be avoided in the near future. Still unknown, for example, is whether that threshold is simply a function of the spatial scale and intensity of the forcing perturbation, of the quality of the perturbation [see, for example, the apparently more severe biotic effects of increased seasonality as opposed to simple changes in mean annual temperature (20)] or whether feedbacks involving, for example, the compounding of perturbations (21), or the disruption of biotic interactions or community structures come into play.

In principle, threshold effects should be detectable in time series around mass extinction events, and this would be especially valuable in light of the cumulative extinction processes operating today. The demonstrable selectivity of extinctions raises the issue of weakening vs. hardening of the biota if unfavorable conditions are imposed over a protracted interval: as the most vulnerable taxa such as endemic species are lost, under what circumstances will the extinction-resistant residue withstand further stresses, and when will they give way to the mass-extinction regime? A hardening process may underlie the pulse of extinction near the onset of Pleistocene glaciation and the dearth of extinction thereafter (22) (the end-Pleistocene megafaunal extinction is probably a different issue), and we need a better understanding of exactly what separates such events from the major mass extinctions, and to what extent such hardening processes undermine linear projections of present-day extinction estimates to future losses. We can simply appeal again to the spatial scale, intensity, or quality of the perturbation, or to the quality of the perturbation, but this leads us back to the uncertain nature of the threshold, whether it is graded or a step-function, and its potential variation among taxa, communities, and regions.

Spatial Patterns

Most paleontological analyses of mass extinctions have neglected the spatial dimension, tending to focus instead either on single stratigraphic sections or regions, or on synoptic global databases. Both scales have been extremely productive, but the global biota is spatially complex, with diversity gradients and hotspots (e.g., refs. 23–26) and concomitant variation in the generation and persistence of evolutionary novelties and higher taxa (27) [although the relation to species-level evolutionary dynamics is still unclear (28, 29)]. Paleontological analyses that contain a spatial component, for example regarding regional extinction events at all scales (30) or the biogeographic fabric of postextinction evolutionary patterns, therefore would be especially valuable with reference to present-day and future processes. Biotic interchanges in the paleontological record, such as the late Cenozoic responses to the joining of North and South America after the final uplift of the Panama Isthmus, or the opening of transpolar interchange between Pacific and Atlantic, clearly document asymmetries in biotic interchanges that correspond to regional differences in extinction intensities (31, 32). These paleontological findings that regions suffering greater losses were more heavily invaded is an important verification and extension into deep time of observations made in modern communities (33).

Geographical analyses of mass extinctions and their aftermath, however, show that more complex dynamics may sometimes operate. For example, although K-T extinction intensities were statistically homogeneous for marine mollusks on a global scale (except perhaps for shallow, clear-water tropical platforms), the evolutionary and biogeographic response was decidedly inhomogeneous. Of the four regions analyzed as time series (34), only the North American Gulf and Atlantic Coastal Plain showed a prolific but short-lived burst of diversification by several clades [termed "bloom taxa" (35)] that were quiescent elsewhere and was significantly more subject to postextinction biotic invasions. Although further analyses are desirable, particularly from a phylogenetic standpoint, these patterns are likely to be robust: they hold whether the bloom taxa are treated as a proportion of the biota or as raw species numbers when the K-T bottleneck is taken into account (34). Furthermore, neither burst nor excess invasion appears in an extensive new analysis of an important fauna in the earliest Tertiary of northern Europe (36), which is the region most likely to conform to North America by reason of proximity and climatic similarity.

Understanding these paleontological patterns is particularly pressing in light of the massive biotic interchanges that are currently being directly or indirectly mediated by human activities. Why was North America subject to more intense invasion after the K-T event despite its unexceptional (if severe) extinction intensities? This response implies a nonlinear between extinction and invasion intensities, or perhaps simply a threshold above which the relation breaks down. Another possibility is that when losses approach paleontological mass-extinction levels (that is, 50% of the relatively abundant and widespread genera) or are globally both severe and homogeneous, qualitative as well as quantitative losses determine the probability of the evolutionary excursions and invasions seen in North America: the identity of the victims and not just their numbers becomes particularly important. The functional role of taxa lost from each of the regional biotas will be difficult to assess rigorously, but divergent regional responses to homogeneous extinction intensities provide a natural experiment sufficiently rich in potential insights to demand further investigation. Lockwood's analyses[†] showing no relation between abundance and survivorship in this fauna undermines one of the simplest hypotheses: that preferential removal of abundant and thus dominant taxa was masked by a strictly taxonomic approach (although a detailed parallel analysis of other regions is required for a definitive test, of course).

The evolutionary effects of biotic homogenization may depend in part on how it is achieved. Homogenization via elimination of endemics will leave a residue of already widespread taxa that may be relatively resistant to geographic isolation and rapid diversification, whereas homogenization via range expansion may more readily promote the origin and diversification of new endemic taxa. Invaders are not drawn randomly from the source biota, however (34, 37), and this bias could itself channel subsequent evolution into narrower pathways among regions than would otherwise be expected.

Spatial effects may be important in finer scales as well. For example, in North America within-habitat molluscan diversity appears to recover within a few million years after the K-T extinction (38), but total regional diversity evidently does not reach preextinction levels until roughly 10 million years after the event (34, 35). Although this result needs to be verified elsewhere, and tested more rigorously for sampling artifacts, it suggests that beta diversity, the differentiation of local faunas among habitats and along environmental gradients, takes longer to recover than alpha, i.e., local, diversity.

Continuity and Creativity

Mass extinctions have never entirely reset the evolutionary clock: even the huge losses at the end of the Permian, which appear to have permanently restructured marine and terrestrial communities, left enough taxa and functional groups standing to seed the recovery process without the origin of new phyla (39). One key to understanding the past and future evolutionary role of extinctions will involve the factors that permit the persistence of certain biological trends or patterns—e.g., net expansion or contraction of clades or directional shifts in morphology—in the face of extensive taxonomic loss and ecological disruption. Besides extinction, at least four evolutionary patterns can be seen in the fossil record. These are: (*i*) unbroken continuity, (*ii*) continuity with setbacks, (*iii*) survival without recovery ("dead clade walking"), and (*v*) unbridled diversification.

Unbroken Continuity. Some large-scale patterns withstood one or more of the Big Five extinctions with little disruption. These include the continued dominance of reefs by rugose and tabulate corals and stromatoporoid sponges across the Ordovician-Silurian boundary (40, 41), the escalation of morphological responses seen in molluscan shells to increased predation intensity across the K-T boundary (42), the prolonged Paleozoic decline of trilobites (43), and the onshore-offshore expansions and retreats of a number of post-Paleozoic marine orders (44).

Continuity with Setbacks. Other trends suffer setbacks—presumably owing to the contrast between mass extinction and "normal" selectivities—but then resume their long-term trajectories. These include rising cheilostome bryozoan dominance relative to cyclostomes (45), the ecological expansion of angiosperms (46, 47) although this may be more an ecological than an evolutionary setback, and the spread to greater burrowing depths by veneroid bivalves,[‡] all at the K-T boundary, the early Paleozoic spread of suspension-feeding bivalves to offshore shelf environments (48), and the overall Paleozoic increase in suture complexity in ammonoids (49). An important open question amenable to direct testing and simulation is whether such setbacks are generally a simple byproduct of high extinction intensities (if the extremes of the morphospace volume are sparsely occupied, for example, then random extinction could clear those portions), or represent selection against the traits being maximized under low extinction intensities.

Dead Clade Walking. Clade survival is no guarantee that preextinction trends will persist or be reasserted in the postextinction setting. Each extinction has examples of clades that survived the extinction event only to fall into a marginal role or eventually disappear (dead clade walking). These include bellerophontid snails (7) and prolecanitid ammonoids at the Permo-Triassic boundary (50), the brachiopod order Spiriferoida after the end-Triassic extinction (51), and the planktic foraminiferal Zeauvigerina lineage after the K-T event (52). Such lingering demises need to be tested against stochastic attrition, of course (43). My preliminary, unpublished analysis suggests that the intervals after mass extinctions tend to be significantly enriched in taxa that failed to cross the next stage boundary, relative to other intervals before the extinction event; in other words more clades that survived a mass extinction tend to dwindle or disappear shortly after the event than would be expected by chance. Also intriguing is the geographic variation in the proportion of dead clade walking taxa across the K-T boundary, with values highest not in North America (which makes an interesting statement on the impact of the greater influx of invaders there—they followed extinctions but did not drive them), but in the tropical Indian Ocean.

These diverse postextinction trajectories again demonstrate that analysis of the evolutionary role of extinctions must include much more than taxonomic survivorship at the event itself. We need to understand why some clades, and some polyphyletic trends such as escalation of antipredatory defenses, persist uninterrupted across the extinction event, why others stumble but recover their preextinction trajectory, and still others survive

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[‡] Lockwood, R. (1998) *Geol. Soc. Am. Abstr. Programs* 30, A-286.

but never recover. All of the patterns discussed so far strongly attest that postextinction evolutionary processes involve not simply unbridled radiation (see below), but a sorting of survivors in the postextinction world. At this early stage, many alternative hypotheses are feasible and the relative power of the alternatives may vary among different situations. The most obvious is the taxonomic breadth of the trend: all else being equal, any evolutionary trend that advances along a broad ecological or taxonomic front is less likely to be halted by extinction. Although this is surely a factor, it is unlikely to be sufficient in all cases, because many trends are fairly circumscribed phylogenetically, as in the bryozoan and veneroid examples given above.

Given the discordance in selectivity between times of high and low extinction intensities, another factor in the persistence of trends is likely to be the strength of association between traits involved in trends and those related to survivorship. The role of this macroevolutionary linkage in promoting the long-term persistence of trends is virtually unexplored. A final potential explanation is even more context-specific, that the differential persistence of trends depends less on the intrinsic traits of clades than on the strong variation recorded in postextinction recovery (*i*) among ecosystems, e.g., the more rapid recovery of diversity in oceanic plankton vs. marine benthos (53, 54) (with potentially important implications for the relative persistence of mineral and nutrient cycles); (*ii*) across ecological scales, e.g., discordances in the time to recovery of local vs. global diversity (as mentioned above, with potentially important implications for the accumulation of biological diversity and the development of spatial structure); and (*iii*) among regions in clade dynamics and biotic interchanges, e.g., the concentration of bloom taxa and postextinction invasions in particular areas (with potentially important implications for the persistence and recovery of local biotas and intrerregional source-sink dynamics).

Unbridled Diversification. The most dramatic and creative evolutionary role of mass extinctions is the promotion of postextinction diversifications, typified most vividly by the exuberant radiation of the mammals after the demise of the dinosaurs and other reptilian clades at or near the K-T boundary. Postextinction bursts of diversification have been extensively discussed and documented for many extinction events, both morphologically and at several taxonomic levels (6, 39, 41, 55–58). Therefore, before returning to the need for further analysis of geographic variation in evolutionary dynamics, I will make only two further points, on predictability and time scales.

Predictability. Although the evolutionary response to mass extinction has sometimes been depicted simply in terms of the reoccupation of preextinction adaptive peaks ("reinventing the ecological wheel," ref. 59), evolution is both too opportunistic and too constrained by inherited body plans for this to be wholly true. Striking convergences in form and habit are, of course, a major theme in evolution, but postextinction dynamics are complicated by near-simultaneous radiation of multiple clades [with the powerful incumbency advantage at stake (32)], the distinct ecological context of each postextinction interval, and the raw material provided by surviving lineages. These effects can be seen in the incomplete congruence of successive occupations of morphospace after extinction events (60, 61).

To drive home these important but somewhat abstract points on the long-term prospects for evolutionary replacements, consider the Cenozoic history of birds. The large, flightless phorusrhacid and diatrymid birds, probably the top carnivores of early Cenozoic terrestrial communities (62, 63), interfered with the triumphant mammalian ascent to center stage in the post-dinosaurian world, and probably were not replaced by an exact mammalian analog once they disappeared. Note also that these carnivorous birds opportunistically converged on theropod dinosaurs rather than adhering to the pterosaur models that might have been the most likely targets for convergence given a flying avian starting point (62). Over the course of Cenozoic diversification, other birds did assume modes of life similar to those vacated by pterosaurs: skimmers may roughly correspond to *Tropeognathus* with its keeled jaws, swallows and swifts to *Pterodactylus* with its similar size and wing proportions, flamingos to *Pterodaustro* with its bristling array of fringe-like teeth, and perhaps even condors to the enormous *Quetzlcoatlus* (64, 65). This does not mean, however, that birds—or even birds plus bats—managed to occupy the full range of pterosaur habits (66). Equally important, the granivorous habit so important in modern birds evidently represents a novel expansion of bird ecospace relative to their supposed pterosaur models (see ref. 66 on the avian trophic diversification). There may be good functional or ecological reasons for this (e.g., was the Mesozoic seed bank as rich and dependable a resource as in the angiosperm-dominated Cenozoic?), just as there seems to have been for the absence of baleen-like filter-feeding in Mesozoic marine reptiles (67), but such constraints and contingencies are precisely the factors that prevent a given set of clades at a given time from fully overlapping the evolutionary pathways of their predecessors. Attempts to predict evolutionary behavior after major extinction events can only operate in broad generalities, and always with the caveat, "expect the unexpected."

Time Scales. The fossil record shows that destructive and generative aspects of extinction generally operate in different time frames, as many authors have pointed out (2, 41, 68). The biotic impoverishment and homogenization necessarily precedes the evolutionary response, and there is surprisingly little hard evidence for major evolutionary innovations within a major extinction episode. Even for apparently protracted or multistep extinctions that see origination within the extinction interval, such as the end-Ordovician or end-Permian episodes, "little biological innovation is apparent" (41).

Recoveries of different biomes, clades, or communities may have different postextinction lag times; for example, broadly defined "reef" systems lag behind oceanic plankton systems (see ref. 2 for discussion). Whether these lags reflect a general property of large-scale diversity dynamics (13, 69), sampling and other biases (6, 70), the duration or intensity of environmental stresses (71), a protracted process of assembling new ecological communities (2, 72), or evolutionary waiting times set by intrinsic diversification rates (73) awaits further comparative analysis.

Geography. The spatial dimension is important not only to extinction selectivity and postextinction interchange, but to long-term evolutionary dynamics in a postextinction world. Certain habitats and regions, such as onshore marine settings (44), and the tropics in both marine (27) and terrestrial (74–76) settings, appear to be important sources of postextinction evolutionary novelty, but the implications of this nonrandom creativity have only begun to be explored. On finer geographic scales, a systematic search for diversity hotspots in the geologic record to test for their long-term persistence and evolutionary significance would be valuable. For example, is the end-Ordovician extinction of brachiopods and other benthic taxa in North America a potential case study in the destruction and later refurbishment of a diversity hotspot? North America straddled the equator and harbored a rich biota of endemic taxa in the epicontinental sea that occupied the center of the continent. Oscillating climates and fluctuating sea levels virtually eliminated this and other interior seaways and their biotas, and the postextinction interval saw an invasion pulse as taxa from outside the region expanded to occupy the returning favorable habitats (77, 78).

Tracking such hotspots and other crucibles of biotic novelty over evolutionary time might help to prioritize targets for both research and conservation efforts in the near future. Do relatively localized hotspots primarily contribute taxonomic richness to the global biotic inventory, or are they also important reservoirs of biodisparity, that is morphological richness? The evolutionary importance of the answer will depend in part on the mean lifetime of such hotspots, and the extent to which novelties that arise in hotspots tend to spread elsewhere, as has been documented for novelties that originated in onshore environments or within tropical latitudes (27, 44, 74–76). For these and many other questions, paleontology can be a rich source of natural experiments in macroevolutionary dynamics before, during, and after perturbations of widely varying intensities and durations.

Conclusion

I would not go far wrong in saying that the most dramatic evolutionary effects of mass extinctions can be epitomized in just four words: they remove successful incumbents. But going beyond what amounts to a concession to contingency, what are the lessons of the past that transcend the specific mechanisms, intensities, and participants of earlier events?

(*i*) Mass extinctions happen. The fossil record provides ample evidence that even the more widespread and species-rich clades, ecosystems, and biogeographic provinces are not infinitely resilient. Biogeochemical and other data are accumulating on the concomitant breakdown of nutrient cycling and other ecosystem-level processes (53), and the links among the collapse and recovery of taxonomic diversity, morphological, or functional disparity and ecosystem function should be a high priority.

(*ii*) Survivorship during mass extinctions need not be closely related to many aspects of biological success as measured during "background" times. An understanding of the evolutionary role of mass extinctions requires continued analysis of why well-established incumbents are lost, surely at least in part a function of the spatial scale of perturbations, and the long-term consequences of such losses.

(*iii*) Extinction itself promotes biotic interchange. Asymmetries in ancient biotic interchange generally appear to reflect geographic differences in extinction intensity. The K-T extinction shows, however, that although biotic interchanges pervade the postextinction world, simple linear relationships can break down to produce unexpected source-sink patterns.

(*iv*) The evolutionary response to mass extinction is slow on human time scales, difficult to predict owing to the contingencies of postextinction conditions including the identity and evolutionary dynamics of the survivors, and geographically heterogeneous. Each of these complications, however, is amenable to comparative paleontological analysis and modeling, with the attendant opportunities for detecting patterns, testing hypotheses, and drawing lessons relevant to the future of evolution.

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1. Sepkoski, J. J., Jr. (1993) *Paleobiology* **19,** 43–51.
2. Jablonski, D. (1995) in *Extinction Rates*, eds. May, R. M. & Lawton, J. H. (Oxford Univ. Press, Oxford), pp. 25–44.
3. McKinney, M. L. (1997) *Annu. Rev. Ecol. Syst.* **28,** 495–516.
4. Jablonski, D. & Raup, D. M. (1995) *Science* **268,** 389–391.
5. Jablonski, D. (1989) *Philos. Trans. R. Soc. London B* **325,** 357–368.
6. Jablonski, D. (2001) in *Evolution on Planet Earth: The Impact of the Physical Environment*, eds. Lister, A. & Rothschild, L. (Academic, London), in press.
7. Erwin, D. H. (1996) in *Evolutionary Paleobiology*, eds. Jablonski, D., Erwin, D. H. & Lipps, J. H. (Univ. of Chicago Press, Chicago), pp. 398–418.
8. Raup, D. M. (1984) in *Patterns of Change in Earth Evolution*, eds. Holland, H. D. & Trendall, H. F. (Springer, Berlin), pp. 5–14.
9. Raup, D. M. (1994) *Proc. Natl. Acad. Sci. USA* **91,** 6758–6763.
10. Kitchell, J. A., Clark, D. L. & Gombos, A. M., Jr. (1986) *Palaios* **1,** 504–511.
11. Norris, R. D. (1991) *Paleobiology* **17,** 388–399.
12. Keller, G., Adatte, T., Hollis, C. J., Ordonez, M., Zambrano, I., Jimenez, N., Stinnesbeck, W,. Aleman, A. & Hale-Erlich, W. (1997) *Mar. Micropal.* **31,** 97–133.
13. Sepkoski, J. J., Jr. (1998) *Philos. Trans. R. Soc. London B* **353,** 315–326.
14. McKinney, M. L. (1998) in *Biodiversity Dynamics*, eds. McKinney, M. L. & Drake, J. A. (Columbia Univ. Press, New York), pp. 1–16.
15. Gilinsky, N. L. (1998) in *Biodiversity Dynamics*, eds. McKinney, M. L. & Drake, J. A. (Columbia Univ. Press, New York), pp. 162–184.
16. McKinney, M. L. (1985) *Paleobiology* **11,** 227–233.
17. Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. (1995) *Science* **269,** 347–350.
18. Rosen, B. R. & Turnsek, D. (1989) *Mem. Assoc. Australas. Palaeont.* **8,** 355–370.
19. Russell, G. J., Brooks, T. M., McKinney, M. L. & Anderson, C. G. (1998) *Conserv. Biol.* **12,** 1365–1376.
20. Ivany, L. C., Patterson, W. P. & Lohmann, K. C. (2000) *Nature (London)* **407,** 887–890.
21. Paine, R. T., Tegner, M. J. & Johnson, E. A. (1998) *Ecosystems* **1,** 535–545.
22. Jackson, J. B. C. (1995) in *Extinction Rates*, eds. May, R. M. & Lawton, J. H. (Oxford Univ. Press, Oxford), pp. 45–54.
23. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. (2000) *Nature (London)* **403,** 853–858.
24. Reid, W. V. (1998) *Trends Ecol. Evol.* **13,** 275–280.
25. Gaston, G. J. & Williams, P. H. (1996) in *Biodiversity*, ed. Gaston, K. J. (Blackwell, Oxford), pp. 202–229.
26. Roy, K., Jablonski, D. & Valentine, J. W. (1996) *Philos. Trans. R. Soc. London B* **351,** 1605–1613.
27. Jablonski, D. (1993) *Nature (London)* **364,** 142–144.
28. Crame, J. A. & Clarke, A. (1997) in *Marine Biodiversity*, eds. Ormond, R. F. G., Gage, J. D. & Angel, M. V. (Cambridge Univ. Press, Cambridge), pp. 258–273.
29. Flessa, K. W. & Jablonski, D. (1996) in *Evolutionary Paleobiology*, eds. Jablonski, D., Erwin, D. H. & Lipps, J. H. (Univ. of Chicago Press, Chicago), pp. 376–397.
30. Miller, A. I. (1998) *Science* **281,** 1157–1160.
31. Vermeij, G. J. (1991) *Science* **253,** 1099–1104.
32. Jablonski, D. & Sepkoski, J. J., Jr. (1996) *Ecology* **77,** 1367–1378.
33. Williamson, M. (1996) *Biological Invasions* (Chapman & Hall, London).
34. Jablonski, D. (1998) *Science* **279,** 1327–1330.
35. Hansen, T. A. (1988) *Paleobiology* **14,** 37–51.
36. Heinberg, C. (1999) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **154,** 87–106.
37. McKinney, M. L. & Lockwood, J. L. (1999) *Trends Ecol. Evol.* **14,** 450–453.
38. Hansen, T. A., Farrell, B. R. & Upshaw, B. III (1993) *Paleobiology* **19,** 251–269.
39. Erwin, D. H., Valentine, J. W. & Sepkoski, J. J., Jr. (1987) *Evolution* **41,** 1177–1186.
40. Droser, M. L., Bottjer, D. J. & Sheehan, P. M. (1997) *Geology* **25,** 167–170.
41. Erwin, D. H. (1998) *Trends Ecol. Evol.* **13,** 344–349.
42. Hansen, T. A., Kelley, P. H., Melland, V. D. & Graham, S. E. (1999) *Geology* **27,** 1139–1142.
43. Raup, D. M. (1981) *Acta Geol. Hispanica* **16,** 25–33.
44. Jablonski, D. & Bottjer, D. J. (1990) in *Causes of Evolution*, eds. Ross, R. M. & Allmon, W. A. (Univ. of Chicago Press, Chicago) pp. 21–75.
45. McKinney, F. K., Lidgard, S., Sepkoski, J. J., Jr., & Taylor, P. D. (1998) *Science* **281,** 807–809.
46. Boulter, M. C., Spicer, R. A. & Thomas, B. A. (1988) in *Extinction and Survival in the Fossil Record*, ed. Larwood, G. P. (Oxford Univ. Press, Oxford), pp. 1–36.
47. Wing, S. L. & Boucher, L. D. (1998) *Annu. Rev. Earth Planet. Sci.* **26,** 379–421.
48. Miller, A. I. (1988) *Hist. Biol.* **1,** 251–273.
49. Saunders, W. B., Work, D. M. & Nikovaeva, S. V. (1999) *Science* **286,** 760–763.
50. Page, K. N. (1996) in *Ammonoid Paleobiology*, eds. Landman, N. H., Tanabe, K. & Davis, R. A. (Plenum, New York), pp. 755–794.
51. Ager, D.V. (1987) *Palaeontology* **30,** 843–857.
52. Huber, B. T. & Boersma, A. (1994) *J. Foram. Res.* **24,** 268–287.
53. D'Hondt, S., Herbert, T. D., King, J. & Gibson, C. (1996) *Geol. Soc. Am. Spec. Paper* **307,** 303–317.
54. Conway Morris, S. (1998) *Philos. Trans. R. Soc. London B* **353,** 327–345.
55. Patzkowsky, M. E. (1995) *Paleobiology* **21,** 440–460.
56. Foote, M. (1997) *Annu. Rev. Ecol. Syst.* **28,** 129–152.
57. Eble, G. J. (1998) in *Biodiversity Dynamics*, eds. McKinney, M. L. & Drake, J. A. (Columbia Univ. Press, New York), pp. 132–161.
58. Erwin, D. H. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5399–5403.
59. Eldredge, N. (1997) in *Biodiversity: An Ecological Perspective*, eds. Abe, T., Levin, S. A. & Higashi, M. (Springer, Berlin), pp. 59–73.
60. McGhee, G. R., Jr. (1999) *Theoretical Morphology* (Columbia Univ. Press, New York).

61. Foote, M. (1999) *Paleobiology* **25,** Suppl. to no. 2, 1–115.
62. Feduccia, A. (1999) *The Origin and Evolution of Birds* (Yale Univ. Press, New Haven, CT), 2nd Ed.
63. Witmer, L. M. & Rose, K. D. (1991) *Paleobiology* **17,** 95–120.
64. Rayner, J. M. V. (1989) *Trans. R. Soc. Edinburgh Earth Sci.* **80,** 311–320.
65. Wellnhofer, P. (1991) *The Illustrated Encyclopedia of Pterosaurs* (Salamander, London).
66. Zweers, G. A., Vanden Berge, J. C. & Berkhoudt, H. (1997) *Zoology* **100,** 25–57.
67. Collin, R. & Janis, C. M. (1997) in *Ancient Marine Reptiles*, eds. Callaway, J. M. & Nicholls, E. L. (Academic, San Diego), pp. 451–466.
68. Myers, N. (1996) *Environmentalist* **16,** 37–47.
69. Kirchner, J. W. & Weil, A. (2000) *Nature (London)* **404,** 177–180.
70. Smith, A. B. (1994) *Systematics and the Fossil Record* (Blackwell, Oxford).
71. Sepkoski, J. J., Jr. (1984) *Paleobiology* **10,** 246–267.
72. Talent, J. A. (1988) *Senckenb. Lethaea* **69,** 315–368.
73. Stanley, S. M. (1990) *Paleobiology* **16,** 401–414.
74. Askin, R. A. & Spicer, R. A. (1995) in *Effects of Past Global Change on Life*, Board on Earth Sciences and Resources, National Research Council (Natl. Acad. Press, Washington, DC), pp. 156–173.
75. Meyen, S. V. (1992) *Sov. Sci. Rev. G Geol.* **1,** 39–70.
76. Judd, W. S., Sanders, R. W. & Donoghue, M. J. (1994) *Harvard Papers Bot.* **5,** 1–51.
77. Sheehan, P. M. & Coorough, P. J. (1990) *Geol. Soc. London Mem.* **12,** 181–187.
78. Harper, D. A. T. & Rong, J.-Y. (1995) *Mod. Geol.* **20,** 83–100.

Lessons from the past: Biotic recoveries from mass extinctions

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Although mass extinctions probably account for the disappearance of less than 5% of all extinct species, the evolutionary opportunities they have created have had a disproportionate effect on the history of life. Theoretical considerations and simulations have suggested that the empty niches created by a mass extinction should refill rapidly after extinction ameliorates. Under logistic models, this biotic rebound should be exponential, slowing as the environmental carrying capacity is approached. Empirical studies reveal a more complex dynamic, including positive feedback and an exponential growth phase during recoveries. Far from a model of refilling ecospace, mass extinctions appear to cause a collapse of ecospace, which must be rebuilt during recovery. Other generalities include the absence of a clear correlation between the magnitude of extinction and the pace of recovery or the resulting ecological and evolutionary disruption the presence of a survival interval, with few originations, immediately after an extinction and preceding the recovery phase, and the presence of many lineages that persist through an extinction event only to disappear during the subsequent recovery. Several recoveries include numerous missing lineages, groups that are found before the extinction, then latter in the recovery, but are missing during the initial survival–recovery phase. The limited biogeographic studies of recoveries suggest considerable variability between regions.

However much one may mourn the passing of trilobites, conodonts, ammonoids, richtofenid brachiopods, and even dinosaurs, there is no denying the profound evolutionary impetus mass extinctions have provided to the history of life. Mass extinctions create new evolutionary opportunities and redirect the course of evolution. During the past two decades, paleontologists have focused great effort on the patterns, rates, and causes of various mass extinctions. Our understanding of these events has improved greatly, but postextinction rebounds have received far less attention. This lack of attention is unfortunate, for the available detailed empirical studies of recoveries have revealed great complexity to postextinction rebounds, raising questions about the applicability of many models of evolutionary dynamics. Analysis of these extensive biotic disturbances provides detailed information about how ecosystems respond to perturbations and the processes underlying diversification, and insights into what we might plausibly expect from our current biodiversity crisis. In this paper, I will place recovery studies within the context of models of biodiversity dynamics, review the results of both modeling work and empirical studies of specific postextinction recoveries, consider the general patterns that can be derived from a comparative study of recoveries, and close with a discussion of the evolutionary significance of biotic recoveries.

Recoveries and Biodiversity Dynamics

Paleontological discussions of postextinction recoveries have been heavily influenced by models of evolutionary dynamics, particularly competition-driven models governed by the Lotka–Volterra equations and the equilibrial models from MacArthur and Wilson's theory of island biogeography (ref. 1, reviewed in ref. 2). Coupled logistic models have been applied to the dynamics of clades from the fossil record and the patterns of recoveries after mass extinctions (3–6). The models suggest that recoveries will follow a sigmoidal increase to a new equilibrium as survivors radiate into a now-empty ecospace. The sigmoidal shape of such a pattern will produce an apparent lag before an exponential increase, with paleontologists noting the exponential phase as the onset of recovery. The duration of the lag should be proportional to the magnitude of the diversity drop (3, 4). Empirical studies have recognized that many mass extinctions are followed by a survival interval, of variable duration, during which little or no diversification is evident, followed by rapid diversification during a recovery phase (7).

Such equilibrium models give rise to the most common definition of postextinction recoveries: the interval of exponential growth immediately after the end of the extinction, and ending with a decline in origination rates to normal levels as a new equilibrium is approached (7–9). Other definitions have been used, however. Paleoecologists focus on the reappearance of apparently normally functioning ecosystems and emphasize community diversity, structure, and complexity (10). Geochemists have invoked carbon isotopes as a proxy for ecosystem behavior (11). Additionally, different clades may recover at different rates during the same event, and the same clade may recover at different rates in different regions. This ecological and biogeographic texture of biotic recoveries robs many definitions and models of their generality but underscores the complexity of the phenomenon.

Although most analyses of biotic recoveries have focused on individual events, a recent paper involves a time series analysis of the offset between origination and extinction peaks and suggested an approximately 10 million-year lag between the two, irrespective of the magnitude of extinction (12). This lag was found even when the five great mass extinctions were excluded from the analysis. Defining recovery as the interval between a peak in extinction intensity and the subsequent peak in origination is novel, and a lag of this magnitude is not immediately evident after any of the great mass extinctions. The time series analysis is plagued by a number of potential problems, however, and the results will have to be confirmed by future work. The time scale used was not updated with recent information, and hence the 10 million-year lag should best be interpreted as a delay of one stratigraphic time unit before the onset of diversification (13). A delay in the onset of recovery of about 5 million years (myr) has long been apparent in the Early Triassic, after the end-Permian mass extinction, and Sepkoski (14) noted the same pattern after other mass extinction events. He suggested several possible explanations, including preservational artifacts,

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Abbreviations: Ma, million years ago; myr, million years; K/T, Cretaceous–Tertiary.

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an artifact resulting from mixing clades with different intrinsic rates of origination (although he discounted this), or a delay in the reestablishment of ecological communities. Variability in origination rates between clades could also produce a synergistic effect in the data (14).

If the results of (12) are valid, they suggest the recovery involves positive feedback, and the active creation of ecospace (12, 13), similar to that recently proposed on the basis of a recent analysis of the delayed recovery of forests in the Early Triassic after the end-Permian mass extinction (15). This pattern of positive feedback is a likely feature of biotic recoveries, irrespective of the validity of ref. 12.

Postextinction Recoveries: Case Studies

In describing extinction–recovery events, I have found it useful to distinguish between rapid perturbations to the system during which no adaptive response is possible and longer-term perturbations during which some lineages may experience adaptive evolution. By analogy with some ecological discussions of disturbance, the former is termed a pulse extinction and the latter a press extinction (16). Sepkoski (2) noted that if perturbations are sufficiently rapid, recovery may begin before the ecosystem fully relaxes to the new expected equilibrium diversity; this pattern is also likely during press extinctions. Continuing perturbations will allow at least some groups to accommodate and potentially diversify while other groups may still be declining (e.g., ref. 17). Several mass extinction episodes, particularly during the Late Devonian, fall into this category.

Five great mass extinction have traditionally been recognized by paleontologists, although there is growing evidence for at least one more event in the Early Cambrian. Recoveries from several other less significant biodiversity crises have also been studied.

Early Cambrian marine faunas are quite distinct from Middle and Late Cambrian assemblages and, although still poorly defined, there is a significant extinction in the latest Early Cambrian (18), possibly in two pulses (19, 20). The reef-building archaeocyath sponges were virtually eliminated, along with calcareous algae and many of the small shelly fossils. Although metazoans do not again play a prominent role in reef formation until the Ordovician, algal and cyanobacterial reefs are common in the Middle and Late Cambrian (21), suggesting that reef ecosystems rebounded relatively quickly but without a significant metazoan component. Other aspects of recovery have not been studied.

Three or four smaller biotic crises during the Late Cambrian and earliest Ordovician are associated with the elimination of many shallow-water trilobites (as well as brachiopods and conodonts) followed by rapid incursions and diversifications of trilobites lineages from deeper waters. Although debate continues over the relative importance of falls in sea level, temperature changes, and other possible causes, the earliest recovery phase is dominated by clades with broad environmental distribution but low relative diversity (number of taxa). Recovery to diverse and specialized faunas occurs within 3 myr (22), with an associated increase in morphologic breadth (23). To the extent that deep-water environments are viewed as refugia, the pattern is consistent with repopulation from refugia followed by diversification.

The end-Ordovician mass extinction [439 million years ago (Ma)] was the second largest of the Phanerozoic but had a far less significant ecological impact than several smaller events. Glaciation and drop in sea level during the first phase of this two-part extinction produced a low-diversity, eurytopic, cool-adapted assemblage that was in turn wiped out during the second phase of the extinction (24). The refined biostratigraphy of this extinction has yielded detailed data on patterns of recovery, emphasizing the independent histories of different clades. Conodonts began expanding from deep water environments, which again served as a refuge, onto the shelf during the interregnum between extinction pulses and formed a low diversity assemblage the earliest Silurian (25). Low-diversity, high-abundance assemblages with broad geographic range are found in the earliest Silurian among graptolites, corals, brachiopods, and some other benthic marine clades (24, 26–28). A number of brachiopod, cystoid, trilobite, and other genera have no fossil record during and immediately after the extinction but then reappear later in the Early Silurian (28–31). These "Lazarus taxa" (32) reveal the persistence of many groups at small population sizes through the extinction and may be significant contributors to the survival fauna. They also serve as a cautionary reminder of the often fragmentary nature of the fossil record of postextinction recoveries. A broad diversification occurs among most groups later in the Early Silurian (24, 26–29). Surprisingly, despite the number of families and genera that disappeared, the extinction had limited ecological effect on reef ecosystems (33).

The Late Devonian extinctions extend from the Givetian through the Devono-Carboniferous boundary, although the major event has been associated with the Frasnian–Fammenian (Late Devonian) extinction (33–36). These repeated extinction pulses complicate the pattern of recovery during this interval, but the general pattern of survival interval followed by diversification appears to hold true for most groups. Sponges, corals, and brachiopods evidently survived in deeper and temperate waters, from which they rediversified (33, 34). Rugose corals are virtually absent from most localities during the early Famennian, followed by a mid-Famennian radiation. A few deep-water Lazarus genera have been recognized, but the new Famennian forms are distinct from those of the underlying Frasnian and their origins obscure. Rugose corals suffer another extinction in the late Famennian but reappear quickly in the earliest Carboniferous and were widespread but of low diversity through much of the Tournasian (37).

There is considerable biogeographic complexity to the recovery (21, 38, 39). A lengthy reef gap evident in North America and western Europe (33) is missing in Asia and Australia, where Famennian reefs were initially dominated by microbes rather than coral or sponges (38). In the Canning Basin of Australia, Wood has described a diverse early Famennian reef composed of surviving calcimicrobes, bryozoans, brachiopods, and an array of sponges (40), casting further doubt on the existence of a reef gap in the aftermath of this extinction. An exquisitely preserved echinoderm fauna from the Fammennian Hongegulung Formation of northwestern China demonstrates the rapid, extensive innovation among blastoids and crinoids (39). These groups did not migrate into Europe and North America until the early Cabroniferous; the delayed migration, probably influenced by the Devono-Carboniferous extinction, produced what appeared to be a long lag before recovery. Such biogeographic studies suggest that apparent delays often reflect biogeographic differences in postextinction habitats, and claims of a global survival–recovery pattern should be approached with caution.

The end-Permian mass extinction (251 Ma) provides perhaps the classic example of a delay before the onset of biotic recovery (41, 42). Paleoecological studies reveal that other than ammonoids, conodonts, and some bivalves, most of the Early Triassic is characterized by low-diversity assemblages of opportunistic forms. Not until the end of the Early Triassic, perhaps 5 myr after the end of the extinction, did signs of broad recovery appear (42–45). Lazarus taxa are particularly notable during the Early Triassic, including up to 30% of the gastropod lineages (16). Gastropods illustrate that surviving the mass extinction is not sufficient to assure continued success. Several lineages, including bellerophontids and subulitids, survived the extinction with little difficulty but quickly disappeared as origination rates increased and other Lazarus forms reappeared. Thus survivorship alone may reveal little about success during the recovery.

The Lazarus taxa return in the latest Early Triassic and Middle Triassic, coincident with diversification among other clades. The Early Triassic recovery lag is the longest documented for any mass extinction, but the causes remain unclear. A continuation of harsh environmental conditions (44–46) (the "environmental damping" of ref. 47), ecological disturbance, and preservation failure have all been implicated (46, 47). The formation of extensive sea-floor carbonate cements into the late Early Triassic supports claims of environmental damping (46), yet the return of stable isotopes and the presence of stenotopic echinoids in shallow waters earlier in the Triassic suggest the lag may in part be ecologic. A potential explanation of delayed recovery that has not been widely explored in the context of biotic recoveries is ecosystem function. One might propose that a prerequisite for recovery would be the rebuilding of sufficient within-trophic-level biodiversity and other aspects of ecosystem function. The relationship between biodiversity and ecosystem function is actively debated, although a recent metanalysis found little support for the idea (48).

Recovery of plants followed a pattern similar to marine groups. The weedy lycopsid *Isoetes* diversified rapidly and dominated many Early Triassic assemblages (49). Looy *et al.* (15) documented a long period of dominantly opportunistic lycopsid pollen into the Spathian stage, when a rapid diversification occurs in Europe. The recovery of this equitorial conifer assemblage corresponds to the recovery of higher latitude peat forests, ending the "coal gap" (50, 51). Retallack (51) has suggested that a pervasive short-lived greenhouse climate could explain the data from plants and paleosols; it may also explain the apparent anoxia in shallow marine settings (35, 45, 46).

The end-Triassic mass extinction (200 Ma) is one of the most significant during the Phanerozoic for both marine and terrestrial groups, but the recovery has been poorly documented. Bivalves, ammonites, brachiopods, crinoids, foraminifera, and ostracodes in Europe show no survival interval but simply a steady diversification over several myr (52), although qualitative data for reefs suggest an early Jurassic interval with missing reefs (21).

Several smaller biotic extinctions and recoveries during the Mesozoic and Cenozoic have received attention, including a recent comparative study of the Early Jurassic Toarcian event and the Late Cretaceous Cenomanian–Turonian bioevent (53). Both extinctions are press extinctions of similar magnitude and involved marine anoxia during relatively high sea level and a greenhouse climate. The biotic recoveries share many characteristics as well: planktic and nektonic clades experienced little extinction and display only limited postextinction diversification. Epifaunal bivalves were well adapted to the anoxic conditions responsible for the extinction and were relatively unaffected. Although there is a clear survival interval after the Cenomanian–Turonian biotic crisis followed by a recovery interval, almost 80% of the species during the recovery interval represent surviving lineages, so there is no evidence for an initial dominance by opportunists (54) except among foraminiferal assemblages in Spain (55). A detailed study of the Andean Basin in South America suggests that the extinction may be exaggerated by a pulse of short-lived endemic taxa (56). Detailed δ^{13}C data show a drop during the anoxic episodes, with the end of the excursions closely correlated with the onset of the recovery interval (ref. 53, but see ref. 55 for a different interpretation). The stratigraphic acuity possible for this event has allowed a detailed reconstruction of the recovery of the pelagic food chain, which has not been possible for other events (57). The calcareous nanoplankton reappear quickly, followed by pelagic foraminifera then benthic foraminifera and dinoflagellates.

The catastrophic nature of the Cretaceous–Tertiary (K/T) extinction (65 Ma) and the abundant early Paleogene sections have yielded an excellent record of biotic recovery. Low-diversity high-abundance opportunists dominate the early record of planktonic foraminifera. A single species of *Guembelitria* is the only species found in the earliest Danian, and all younger planktonic foraminifera are derived from this and one other species. As the recovery progressed, *Guembelitria* gave rise to a number of other opportunistic forms as environmental conditions ameliorated (58, 59). The radiation into diverse habitats is still not well understood (59). Benthic foraminifera from the El Kef section in Tunisia shows a pattern similar to the pelagic forams. The immediate postextinction assemblage is low diversity with shallow-water affinities. This brief survival interval is followed by a gradual increase in the species diversity of the assemblage (60), although this scenario is not accepted by those who question the role of impact in causing the extinction (e.g., ref. 61).

Benthic organisms experienced considerable extinction at the K/T boundary but diversified quickly during the Paleogene. At the Nye Kløv locality in Denmark (62), the first several meters of post-Cretaceous deposits are virtually barren of most groups of fossils other than bourgueticrinid crinoids (this interval corresponds to the very low diversity foram assemblage zone described above). Gradually a more diverse faunal assemblage appears, including many bryozoans and some other echinoderms, and the relative importance of the crinoids wanes. A similar burst of opportunistic molluscan clades has been described from the earliest Danian of the Gulf Coastal Plain (63). But extension of such studies to three other well-studied regions reveals no opportunistic forms at all (64), emphasizing the extreme geographic variability in recovery patterns. Because the level of extinction is similar in all four regions, heightened extinction does not explain the higher number of opportunists in the Gulf Coastal Plain.

Although cheilostome bryozoans gradually replace cyclostomes during the Cretaceous and Tertiary, this long-term pattern is briefly reversed by the greater resilience of cyclostomes to the effects of the K/T mass extinction (65). This resilience appears to reflect not ecological opportunism but a difference in the response to the extinction, which is evident only through analysis of abundance data, rather than simply taxonomic diversity.

Plants have received considerable attention (66–69). A barren interval is found immediately above the extinction horizons in terrestrial sections in western North America, followed by abundant fern spores. Angiosperm-dominated floral assemblages gradually recover over the succeeding 1.5 myr, but an increase in precipitation and a decline in temperature at the boundary complicates analysis of the recovery. Extinction is less apparent in the southern hemisphere, with fewer changes during the recovery.

The complexities of interpreting carbon isotopic studies are evident from recent work on the K/T extinction (11). In contrast to most earlier mass extinctions, the presence of planktic and benthic foraminifera provides a ready means of determining both deep- and shallow-water isotopic signals. The collapse in the differential between the two signals indicates a productivity crisis during the extinction interval. The differential does not appear fully in marine settings until 3 myr after the extinction, but the delayed isotopic recovery evidently does not mean that productivity was reduced for this entire interval. Instead, the evidence suggests that marine productivity recovered within a few hundred thousand years, but the flux of organic material to the deep sea was reduced because of a reorganization in the open ocean ecosystems. The formation of a new ecosystem with multiple trophic levels marked the final recovery of the ecosystem and the final reappearance of the isotopic differential. Analysis of the organic carbon isotope record of C3 plant cuticles, in contrast, has shown that recovery of the terrestrial carbon cycle (and thus atmospheric carbon as well) occurred within about 130,000 years (69).

Postextinction Recoveries: General Results

Several generalities emerge from this review of postextinction rebounds. Initial postextinction faunas often are of low diversity, with abundant eurytopic taxa. This pattern has been documented among late Cambrian trilobites (20), earliest Silurian corals (26), and other groups (27, 28), Late Devonian corals (37), various Early Triassic groups (15, 42, 43, 49), and a number of early Tertiary groups, including pelagic and benthic foraminifera (58–60), some benthic forms (62), and molluscs from the Gulf Coastal plain (63). No apparent survival interval or low-diversity opportunistic assemblages are documented for the end-Triassic mass extinction or the smaller early Jurassic and Cenomanian–Turonian events [with the exception of one locality in Spain (55)]. Jablonski's biogeographic analysis of earliest Tertiary benthic molluscs demonstrates that the opportunistic bursts in one area should not be interpreted as a global signal (64). The ecological and evolutionary influence of the various mass extinctions differ considerably, with no clear connection between the magnitude of extinction and impact. Guild structures were dramatically reduced during the Permo-Triassic extinction (43), and, at least for open-ocean ecosystems, during the Cenomanian–Turonian (57) and end-Cretaceous extinctions (11). A change in guild structure is not evident during the late Cambrian events, although this absence likely reflects a limited understanding of guild structure in late Cambrian ecosystems (22).

Support for the intuitively attractive hypothesis that mass extinctions preferentially remove morphologically complex forms comes from a recent analysis of trends toward increased sutural complexity in Paleozoic ammonoids (70). Sutural complexity increased steadily during this interval, but this trend was reset during the Late Devonian and Permo-Triassic mass extinctions. The simple surviving forms then resumed the trend toward increased complexity. A significant trend among post-Paleozoic molluscs is toward the acquisition of predator-resistant morphologies. In contrast to the ammonoid study, Hansen *et al.* (71) found no evidence for resetting of trends toward less predator-resistant morphologies during the K/T extinction or three other Cenozoic extinctions.

Reefs have been a central focus of much work on mass extinctions and subsequent recoveries. A recent review of reef evolution (21) proposes that the apparent greater susceptibility of reef ecosystems to mass extinctions may actually reflect the greater susceptibility of carbonate platform ecosystems to perturbation. In this view, the apparent lag in reef recovery may reflect a delay in reestablishing an appropriate carbonate platform environment rather than an inherent lag in reef ecosystems. This view is sure to be controversial, in part because not all reefs are found on carbonate platforms, and there may be great practical difficulty in distinguishing between the emergence of carbonate platforms and reef ecosystems. The Frasnian–Fammenian mass extinction and recovery does provide an example of this phenomenon, with diverse reefs reappearing quickly in Canning Basin, Australia but a reef gap is present in North America and Europe (40). This study, and a recent analysis of corals across the K/T event (72), have raised questions about the existence of the widely discussed postmass extinction "reef gaps." Moreover, they suggest that the formation of reef communities is more individualistic than often supposed, and thus any apparent gap is not because of an ecologically imposed delay in recovery.

These results can be compared with proposed models of the recovery process (10, 73). The detailed studies of individual recovery events have demonstrated the variety of roads to success, and these models have explored the possible range of ecologic strategies that could aid in survival and trigger the recovery process. Although both empirical and modeling studies usefully emphasize that all survivors are not eurytopic, generalized, opportunistic taxa (54, 73), the range of proposed survival patterns in the models goes beyond what can be reliably determined from the fossil record. More importantly, such pattern-based models provide few insights into the processes driving the survival and recovery process. There is also substantial doubt about the applicability of even multiphase logistic growth models as explanations for evolutionary recoveries. Although the existence of equilibria is an important issue in diversity dynamics (3–6, 74), it is beyond the scope of this contribution. The apparent inapplicability of logistic growth models to postextinction recovery indicates the need for development of a new class of process-based models involving the synergistic interaction between components of the ecosystem (Fig. 1). In such models, the creation of new species would trigger the creation of new opportunities, producing a positive feedback process.

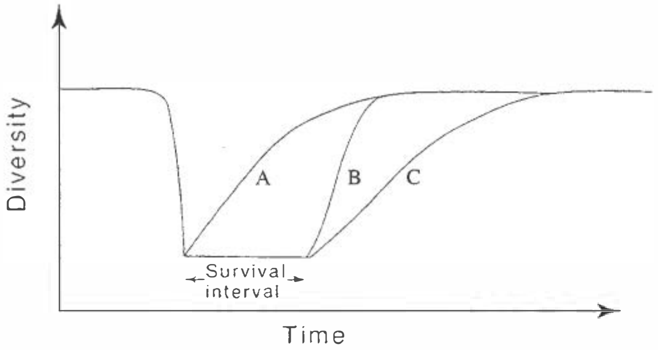

Fig. 1. Expectations from different models of the recovery process. (*A*) A logistic increase in diversity beginning immediately after the end of the mass extinction. (*B*) A postextinction rebound with a lag, followed by positive feedback. (*C*) A logistic diversity increase after a lag survival phase before the onset of recovery.

Clear directions for future research are evident from this overview. Recoveries are still poorly known from almost all of the mass extinctions, and detailed carbon isotope records, useful as a proxy of the health of the carbon cycle, are available for only a few events. There is also a need to expand the repertoire of biogeochemical and environmental proxies for biotic recovery. Nitrogen isotopes, biomarkers, and techniques used by modern ecologists are all worth exploring. Collecting data on the biogeographic structure of recovery is tedious but critical to the development and testing of general recovery models, and the limited biogeographic data clearly illustrate the great spatial variation in recoveries. Virtually absent are detailed phylogenetic studies through extinction, survival, and recovery intervals, yet these are vital to understanding the role and fate of survivors and the locus of recovery. Harries and Little's (53) study of early Jurassic and Late Cretaceous mass extinctions is the only detailed comparative study of biotic recoveries available. Finally, most studies either are paleoecologic or focus on taxonomic diversity. The analysis of ammonid sutural complexity (70) and Foote's studies of crinoids (75) are among the few to explore the changes in morphospace associated with biotic recoveries.

Evolutionary Significance of Postextinction Recoveries

That some mass extinction events have changed the course of evolution is clear, but it is equally obvious that there is no apparent relationship between the magnitude of an extinction and its ecological or evolutionary impact. The end-Permian extinction produced a complete transformation of marine communities, yet even the elimination of perhaps 95% of all marine species did not result in a complete resetting of the evolutionary clock (76). Simulation studies confirm that 80% of the phylogenetic structure can survive a 95% species loss (77). Thus the primary significance of mass extinction may lie in the new ecological patterns that arise during recovery events.

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1. MacArthur, R. H. & Wilson, E. O. (1967) *The Theory of Island Biogeography* (Princeton Univ. Press, Princeton, NJ).
2. Sepkoski, J. J., Jr. (1996) in *Evolutionary Paleobiology*, eds. Jablonski, D., Erwin, D. H. & Lipps, J. (Univ. Chicago Press, Chicago), pp. 211–255.
3. Carr, T. R. & Kitchell, J. A. (1980) *Paleobiology* **6,** 427–443.
4. Sepksoki, J. J., Jr. (1984) *Paleobiology* **10,** 246–267.
5. Benton, M. J. (1997) *Trends Ecol. Evol.* **12,** 490–494.
6. Hewzulla, D., Boulter, M. C., Benton, M. J. & Halley, J. M. (1999) *Philos. Trans. R. Soc. London B* **354,** 463–469.
7. Erwin, D. H. (1998) *Trends Ecol. Evol.* **13,** 344–349.
8. Benton, M. J. (1991) in *The Unity of Evolutionary Biology*, ed. Dudley, E. C. (Dioscorides, Portland, OR), pp. 89–102.
9. Walliser, O. H. (1995) in *Global Events and Event Stratigraphy*, ed. Walliser, O. H. (Springer, Berlin), pp. 7–19.
10. Harries, P. J. & Kauffman, E. J. (1990) in *Extinction Events in Earth History*, eds. Kauffman, E. G. & Walliser, O. H. (Springer, Berlin), pp. 277–298.
11. D'Hondt, S., Donaghay, P. Zachos, J. C., Luttenberg, D. & Lindinger, M. (1998) *Science* **282,** 276–279.
12. Kichner, J. W. & Weil, A. (2000) *Nature (London)* **404,** 177–180.
13. Erwin, D. H. (2000) *Nature (London)* **404,** 129–130.
14. Sepkoski, J. J., Jr. (1998) *Philos. Trans. R. Soc. London B.* **353,** 315–326.
15. Looy, C. V., Brugman, W. A., Dilcher, D. L. & Visscher, H. (1999) *Proc. Natl. Acad. Sci. USA* **96,** 13857–13862.
16. Erwin, D. H. (1996) in *Evolutionary Paleobiology*, eds. Jablonski, D., Erwin, D. H. & Lipps, J. (Univ. Chicago Press, Chicago), pp. 398–418.
17. Budd, A. F. & Johnson, K. G. (1999) *Paleobiology* **25,** 188–200.
18. Brasier, M. D. (1995) in *Global Events and Event Stratigraphy*, ed. Walliser, O. H. (Springer, Berlin), pp. 113–138.
19. Zhuravlev, A. Y. (1996) in *Biotic Recovery from Mass Extinction Events*, ed. Hart, M. B. (Geology Society of London, London), Special Publication 102, pp. 79–96.
20. Zhuravlev, A. Y. & Wood, R. A. (1996) *Geology* **24,** 311–314.
21. Wood, R. (1999) *Reef Evolution* (Cambridge Univ. Press, Cambridge, U.K.).
22. Westrop, S. R. & Cuggy, M. B. (1999) *J. Paleontol.* **73,** 337–354.
23. Sundberg, F. A. (1996) *Paleobiology* **22,** 49–55.
24. Sheehan, P. M. & Coorough, P. J. (1990) in *Palaeozoic Palaeogeography and Biogeography*, eds. McKerrow, W. S. & Scotese, C. R. (Geology Society Memoir 12, London), pp. 181–187.
25. Armstrong, H. A. (1996) in *Biotic Recovery from Mass Extinction Events*, ed. Hart, M. B. (Geology Society of London, London), Special Publication 102, pp. 105–107.
26. Elias, R. J. & Young, G. A. (1998) *Palaios* **13,** 98–112.
27. Kaljo, D. (1996) in *Biotic Recovery from Mass Extinction Events*, ed. Hart, M. B. (Geology Society of London, London), Special Publication 102, pp. 127–133.
28. Harper, D. T. & Rong, J. Y. (1995) *Mod. Geol.* **20,** 83–100.
29. Fortey, R. A. (1989) *Philos. Trans. R. Soc. London B* **325,** 327–355.
30. Rong, J. Y. & Harper, D. A. T. (1999) *Geol. J.* **34,** 321–348.
31. Rong, J. Y. & Zhan, R. B. (1999) *Science in China, Ser. D* **42,** 553–560.
32. Jablonski, D. (1986) in *Dynamics of Extinction*, ed. Elliot, D. K. (Wiley, New York), pp. 183–229.
33. Cooper, P. (1997) *Proc. 8th Int. Coral Reef Symp.* **2,** 1623–1630.
34. McGhee, G. (1996) *The Late Devonian Mass Extinction* (Columbia Univ. Press, New York).
35. Hallam, A. & Wignall, P. W. (1997) *Mass Extinctions and Their Aftermath* (Oxford Univ. Press, Oxford, U.K.).
36. Caplan, M. L. & Bustin, R. M. (1999) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **148,** 187–207.
37. Poty, E. (1999) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **154,** 11–26.
38. Webb, G. E. (1999) *Geology* **26,** 951–954.
39. Lane, N. G., Waters, J. A., Maples, C. G. (1997) *Paleo. Soc. Mem.* **47,** 1–43.
40. Wood, R. (2000) *Palaeontology* **43,** 671–703.
41. Hallam, A. (1991) *Hist. Biol.* **5,** 257–262.
42. Erwin, D. H. (1993) *The Great Paleozoic Crisis* (Columbia Univ. Press, New York).
43. Schubert, J. K. & Bottjer, D. J. (1995) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **116,** 1–39.
44. Twitchett, R. J. & Wignall, P. B. (1996) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **124,** 137–151.
45. Twitchett, R. J. (1999) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **154,** 27–37.
46. Woods, A. D., Bottjer, D. J. Mutti, M. & Morrison, J. (1999) *Geology* **27,** 645–648.
47. Erwin, D. H. (1996) in *Biotic Recovery from Mass Extinction Events*, ed. Hart, M. B. (Geology Society of London, London), Special Publication 102, pp. 223–229.
48. Schwartz, M. W., Brigham, C. A., Hoeksema, J. D., Lyons, K. G., Mills, M. H. & van Mantgem, P. J. (2000) *Oecologia* **122,** 297–305.
49. Retallack, G. J. (1997) *J. Paleontol.* **71,** 500–521.
50. Veevers, J. J., Coagham, P. J. & Shaw, S. E. (1994) *Geol. Soc. Am.* **288,** 187–196.
51. Retallack, G. J. (1999) *GSA Bulletin* **111,** 52–70.
52. Hallam, A. (1996) in *Biotic Recovery from Mass Extinction Events*, ed. Hart, M. B. (Geology Society of London, London), Special Publication 102, pp. 223–229.
53. Harries, P. J. & Little, C. T. S. (1999) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **154,** 39–66.
54. Harries, P. J. (1993) *Cret. Res.* **14,** 563–583.
55. Peryt, D. & Lamolda, M. (1996) in *Biotic Recovery from Mass Extinction Events*, ed. Hart, M. B. (Geology Society of London, London), Special Publication 102, pp. 245–258.
56. Aberhan, M. & Fürsich, F. T. (2000) *J. Geol. Soc. London* **157,** 55–60.
57. Hart, M. B. (1996) in *Biotic Recovery from Mass Extinction Events*, ed. Hart, M. B. (Geology Society of London, London), Special Publication 102, pp. 265–277.
58. Olsson, R. K., Hemleben, C., Berggren, W. A. & Liu, C. A. (1992) *J. Foram. Res.* **22,** 195–213.
59. Koutsoukos, E. A. M. (1996) in *Biotic Recovery from Mass Extinction Events*, ed. Hart, M. B. (Geology Society of London, London), Special Publication 102, pp. 319–335.
60. Speijer, R. P. & Van der Zwaan, G. J. (1996) in *Biotic Recovery from Mass Extinction Events*, ed. Hart, M. B. (Geology Society of London, London), Special Publication 102, pp. 343–371.
61. MacLeod, N. (1996) in *Cretaceous–Tertiary Mass Extinctions*, eds. MacLeod, N. & Keller, G. (Norton, New York), pp. 85–138.
62. Håkansson, E. & Thomsen, E. (1999) *Palaeogeog. Palaeoclimatol. Palaeoecol.* **154,** 67–85.
63. Hansen, T. A. (1988) *Paleobiology* **14,** 37–51.
64. Jablonski, D. (1998) *Science* **279,** 1327–1330.
65. McKinney, F. K., Lidgard, S., Sepkoski, J. J., Jr. & Taylor, P. D. (1998) *Science* **281,** 807–809.
66. Nichols, D. J. & Fleming, R. F. (1996) *Geol. Soc. Am.* **247,** 445–455.
67. Tschudy, R. H. & Tschudy, B. D. (1986) *Geology* **14,** 667–670.
68. Wolfe, J. A. & Upchurch, G. R. (1986) *Nature (London)* **324,** 148–152.
69. Arens, N. C. & Jahren, A. H. (2000) *Palaios* **15,** 314–322.
70. Saunders, W. B., Work, D. M. & Nikovaeva, S. V. (1999) *Science* **286,** 760–763.
71. Hansen, T. A., Kelley, P. H., Melland, V. D. & Graham, S. E. (1999) *Geology* **27,** 1139–1142.
72. Rosen, B. R. (2000) in *Biotic Responses to Global Change*, eds. Culver, S. J. & Rawson, P. F. (Cambridge Univ. Press, Cambridge, U.K.), pp. 164–180.
73. Harries, P. J., Kauffman, E. G. & Hansen, T. A. (1996) in *Biotic Recovery from Mass Extinction Events*, ed. Hart, M. B. (Geology Society of London, London), Special Publication 102, pp. 41–60.
74. Alroy, J. (1998) in *Biodiversity Dynamics*, eds. McKinney, M. L. & Drake, J. A. (Columbia Univ. Press, New York), pp. 232–287.
75. Foote, M. (1996) *Science* **274,** 1492–1495.
76. Erwin, D. H., Valentine, J. W. & Sepkoski, J. J., Jr. (1987) *Evolution (Lawrence, Kans.)* **37,** 1177–1186.
77. Nee, S. & May, R. M. (1997) *Science* **278,** 692–694.

Loss of speciation rate will impoverish future diversity

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Human activities have greatly reduced the amount of the earth's area available to wild species. As the area they have left declines, so will their rates of speciation. This loss of speciation will occur for two reasons: species with larger geographical ranges speciate faster; and loss of area drives up extinction rates, thus reducing the number of species available for speciation. Theory predicts steady states in species diversity, and fossils suggest that these have typified life for most of the past 500 million years. Modern and fossil evidence indicates that, at the scale of the whole earth and its major biogeographical provinces, those steady states respond linearly, or nearly so, to available area. Hence, a loss of *x*% of area will produce a loss of about *x*% of species. Local samples of habitats merely echo the diversity available in the whole province of which they are a part. So, conservation tactics that rely on remnant patches to preserve diversity cannot succeed for long. Instead, diversity will decay to a depauperate steady state in two phases. The first will involve deterministic extinctions, reflecting the loss of all areas in which a species can ordinarily sustain its demographics. The second will be stochastic, reflecting accidents brought on by global warming, new diseases, and commingling the species of the separate bio-provinces. A new kind of conservation effort, reconciliation ecology, can avoid this decay. Reconciliation ecology discovers how to modify and diversify anthropogenic habitats so that they harbor a wide variety of species. It develops management techniques that allow humans to share their geographical range with wild species.

Einstein pointed out that the essence of science consists in connecting state variables to their derivatives. This is true of the state variable called species diversity and the derivative called speciation rate. We must study them together. And no examination can succeed if it does not pay at least passing attention to the other derivative involved—the extinction rate. What determines the number of species alive in a biological province, such as the Neotropics? Answer: The cumulative difference between the creative process of speciation and the destructive process of extinction.

In this paper, I will restrict my attention to the species level of biodiversity (although I do not thus mean to imply that no other level is worthy or interesting). Furthermore, I will use an old-fashioned definition for species—i.e., a collection of organisms that can exchange genes. I know that this definition does not deal adequately with bacteria or interspecies hybrids or jumping genes. But it will lead us to principles that will illuminate the status of an important portion of diversity. And, perhaps, successfully using it may guide us into the world of the multimyriads of species whose diversities we all too often ignore.

Further restricting myself, I will focus on diversity at the grand scale, that of the entire biogeographical province. A biological province is a self-contained region whose species originate entirely by speciation within the region (1). Scales smaller than a province get their species through some form of dispersal, echoing provincial diversity (2). Most probably, every real province has obtained a small proportion of its species by immigration, so the definition constitutes a mathematical ideal. But percentages in excess of 90% are often found, and that should be enough to allow speciation dynamics to dominate the rate processes of a region.

Speciation results from a number of processes, in all of which species are nurseries for other species. Ultimately, that is why the future of speciation is bound up inextricably with the future of species diversity itself. But the connection is even more interesting than that. Both rates—speciation and extinction—depend in part on the geographical range sizes of species. Larger ranges tend to increase the speciation rates and decrease the extinction rates of otherwise similar species. That gives us a parameter to examine—the area of the biogeographical province available to life. Other things being equal, the larger the provincial area, the larger the average species range and speciation rate and the smaller the extinction rate.

What leads evolutionary ecology to its conclusions about range size and the components of diversity dynamics?

- Larger ranges offer larger targets for geographical isolating barriers. The formation of geographical isolates begins the sequence of events leading to allopatric speciation, probably the source of most new species. Thus, a range that is more readily subdivided by geographical barriers will spawn more isolated populations per unit time and have a higher rate of speciation.
- Widespread species also have more genetic variability than narrowly distributed species (3). This may also contribute to the rate of speciation.
- Larger ranges contain species with more subpopulations of their metapopulation (4). Ecologists believe that a complex metapopulation offers some protection from extinction. Although this question continues to be addressed (5), the basic idea seems straightforward and intuitive. When a metapopulation unit becomes extinct, recolonization may occur from surviving units (6). Each unit may survive or become extinct independently of the others. So, the more units, the smaller the probability that all will vanish simultaneously. (Notice that I am not concerned here with the usual question: How does increasing fragmentation of a species range effect extinction probability? Instead, I assume a constant degree of fragmentation and focus on how more fragments alter extinction rate.)
- Larger ranges are more difficult to contain entirely in the area covered by any climatic change or anomaly. Any finite climatic change (such as global warming) or anomaly (such as a severe storm) will affect a finite amount of the earth's surface. If the change covers a species' entire range, and degrades all its appropriate habitat, the species will vanish. And if the anomaly destroys all of the individuals that live within its swath, the

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Abbreviation: my, million years.

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species will also vanish. Thus, the larger the area covered by a species' range, the less chance that range will suffer permanent or temporary obliteration. Again, a larger area diminishes extinction rates.

- Larger ranges produce species with greater total population sizes. And, larger populations may have both lower extinction (7) and higher speciation rates. Many conservation biologists take its effect on extinction largely for granted. They see it as the outcome of the improbability of the simultaneous, stochastic demise of an entire large population. Much work modifies that theory substantially without, however, challenging the relationship (8–12). In addition, evidence from islands supports it (13). Yet, a recent investigation suggests that the literature needs substantial revision to achieve a reliable estimate of how long such extinctions take (14). It concludes that such extinctions may take much less time than we once thought.

No one denies that population size influences speciation rate. However, the direction of its effect is in doubt. At one time, many evolutionists, led by Ernst Mayr (15), believed that small isolated populations provide the crucible for evolution. They believed that getting speciation started is a matter of breaking up coadapted complexes of genes in geographical isolates. If that is correct, small populations would speed up speciation by enhancing statistical sampling accidents. But an alternative view exists. Called "centrifugal speciation" (16), it claims that large populations speed up speciation. Centrifugal speciation also begins with geographical separation of sister populations. But after separation, the larger isolates—not the smaller ones—do the changing. The small ones remain as evolutionary relicts.

According to the centrifugal model of speciation, even the small population sizes of small areas work against evolution. Some theoretical evidence from population genetics supports the idea that small populations cannot evolve quickly (17). So does some (but not all) evidence from real populations (18, 19). And today we know that large populations foster novel gene functions (17). Certainly, genetic variability correlates positively with the total population size of species (3).

We should not allow our unfinished scientific debates to distract us from noticing what we have already learned. Both centrifugal speciation and Mayrian speciation are allopatric modes and emphasize the importance of isolate formation. Isolate formation should proceed faster in larger areas. Finally, no biogeographical patterns suggest that "small" is more productive. Instead, small is a recipe for choking off the speciation process.

The fossil record supports the conclusion that extinction rate and geographical range are inversely related over long periods (20–23). It does not however test the independent significances of the various separate theoretical influences that I mentioned above. The relative importance of these factors remains unknown. Moreover, no one has yet tested the relationship of speciation rate to range size in the fossil record. Although more restricted in time scale, studies of modern areas do support both the correlation of speciation rate with area (24), and the inverse correlation of extinction rate with area (1).

Interprovincial Patterns in Steady States of Species Diversity

The influence of diversity on average species' range size produces a negative feedback system in which species diversity is self-regulating (1). The difference between the speciation and extinction rates of a province ought to approach zero. The net result is a steady-state value of diversity at which new species evolve as fast as established ones become extinct (1).

The steady state of such systems might be only theoretical. The environmental background within which it must be achieved might be too fickle and variable for life ever to attain it. Or its rates could be so slow that it has never been consummated. But paleontological evidence strongly suggests that diversities of regions are often not very far from such steady states (1, 25–27). Alroy's analysis of Cenozoic mammals in North America goes even farther (27). He shows that the dynamic elements of a steady state have been present and active during this time. As diversity fluctuated, speciation rate and extinction rate responded, keeping diversity within narrow bounds. In addition, the two rates intersected over a diversity that did not change significantly during the 65 million year (my) period. Finally, although the per-taxon extinction rate did not vary significantly with diversity, the per-taxon speciation rate did, declining with increases in S and implicating variations in speciation rate as the most responsive component of the system's dynamic stability.

Certainly, periods following a mass extinction are exceptions to the rule of steady states, and so are periods following any major increase in the value of the steady state. During both types of periods, diversity tends to rise more or less monotonically. Nevertheless, during the Phanerozoic Eon, the Earth has experienced only five mass extinctions and a similar number of major increases in steady state (e.g., invasion of the land, invasion of the muddy sea floor, radiation of angiosperms). Each such event appears to have generated no more than 10 my of response in species diversity. Most of the rest of the Phanerozoic Eon is a record of long plateaus interspersed by quick episodes of extinction and recovery (28, 29). Thus, I estimate that species diversity has spent at least 90% of the past 500 my near some steady state. (It would not surprise me to learn that the true proportion is closer to 95% or even 98%.)

The Three Scales of Species–Area Relationships

The theory of provincial diversity predicts that larger provinces will have higher steady state diversities. And they do. But in the power equation that describes species–area curves, their z-values hover near unity (30). Thus, species–area curves among provinces—quite unlike those of islands or of subsamples of a single province—exhibit a lack of curvature in an arithmetic coordinate space.

Other scales of the species–area relationship exist (31). Among islands of an archipelago, species diversity is governed by the dynamics of immigrations to islands—often a slow process, but rarely as slow as speciation. Thus, they have more species than would an equivalent-sized province. This reduces the z-values among islands of an archipelago; they vary between 0.25 and 0.55. Among sample areas within a biogeographical province, species diversity is governed both by the sample of habitats in the area and by rates of local dispersal to sink populations. Such rates are quite high compared with those of immigration. Consequently, they have more species than would an equivalent-sized island. Having more species further reduces the z-values of areas within a single province compared with those of islands; they vary between 0.1 and 0.2. In summary, we see a multiscale picture of species–area curves with regularly varying z-values (Fig. 1).

No mathematical theory explains or predicts the fact that diversity among provinces should be approximately a linear function of area. Yet, several lines of evidence bolster our confidence that the interprovincial z-value is close to unity. First, the linear pattern also exists deep in the fossil record, as we can see from examining some unusually good data about seed plants in the northern hemisphere.

Tiffney and Niklas (32) compiled the numbers of seed plant species known from 11 periods during the past 408 my. The last of them (mid-Miocene) ended some 11.3 my ago. These periods have two characteristics. We know their fossils rather well and we also know the extent to which shallow seas flooded the land during their tenure. The 11 periods have durations from 3.1 to

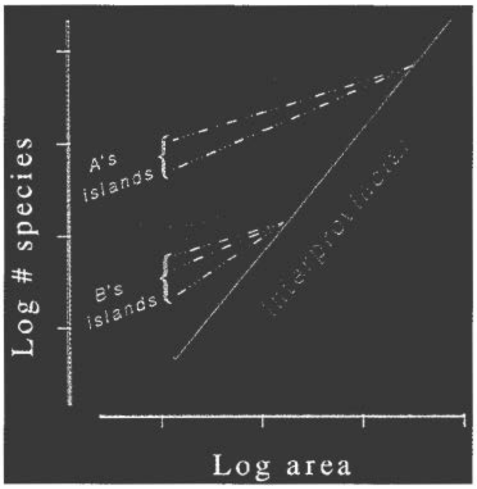

Fig. 1. The three biological scales of species–area curves. Interprovincial curves have z-values near unity; archipelagic curves have z-values that vary from about 0.25 to 0.55; intraprovincial curves have the shallowest logarithmic slopes: their z-values vary from about 0.1 to 0.2. After Rosenzweig (1): Fig. 9.11.

40 my, and cover a total of 225.6 my. (The rest of the 408 my is too poorly known for reliable analysis.)

Displayed against time, these data indicate a substantial rise in species diversity (Fig. 2). The most thorough analyses would also note the long period of little change (*ca.* −330 my to −140 my) and infer the dominance of a steady state during that interval, at least. But area also has a significant effect on these data. The multiple linear regression:

$$\log S = 1.78 + 0.33 \log t + 1.00 \log A$$

$$(R^2 = 0.94;\ p_t = 0.001;\ p_A < 0.05)$$

where t is the amount of time since −408 my.

The most remarkable feature of that equation is the coefficient of area. It is unity, just as it is (approximately) for regressions of modern provincial diversities.

The linear response of diversity to area among provinces appears to explain the total absence of certain groups of native species on small continents, such as ponerine and cerapachyine ants on Hawaii. Two studies give us a picture of the diversity of these subfamilies in tropical southeast Asia, Oceania, and New Zealand (33, 34). These fall nearly on a straight line in arithmetic space ($\log S = -4 + 0.94 \log A$) and enable us to estimate the area of a province that would have a single species (Fig. 3). It is 18,354 km^2. Hawaii, having only 10,378 km^2, falls short.

A similar problem faces bracken-eating insects (35). None live in Hawaii, although the fern does grow there, occupying a range of roughly 1,500 km^2. Based on the species–area curve of such insects in five other provinces, I estimate that one bracken-eating insect species cannot be sustained on less than 10,361 km^2. Obviously, with so few data, such an estimate can give only the order of magnitude of the surface required. However, this is one order greater than what is available.

Finally, echo patterns of species diversity provide additional confidence that we understand the scale differences among species–area relationships. Echo patterns relate local diversity to regional diversity. (In ideal case, regional diversity is equivalent to the diversity of a biogeographical province, although the ideal is rarely met in published examples of the phenomenon.) Based on the scale differences of Fig. 1, theory predicts near-linear Echo patterns (2). Most often, that is what we see (36).

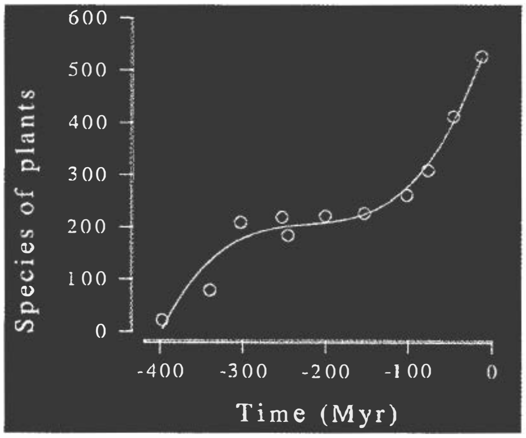

Fig. 2. Species of known fossils of seed plants in the northern hemisphere.

Diversity in Shrunken Natural Provinces

Ecologists question the amount of the earth's nonglaciated terrestrial surface that people now use. Myers *et al.* (37) find that some 88% of the world's richest habitats have been taken. Huston (38) gives a figure of 95% for the world's nonglaciated habitats; Vitousek *et al.* (39) estimate only 40 or 50%. Some of these differences arise from disparate definitions of use, and they are all honest attempts to deal with a somewhat amorphous quantity. But no ecologist would disagree with the qualitative judgment that we are taking a lot.

What does the pervasive impact of civilization do to wild species? It shrinks the area of their province that they can use for themselves. Will that reduce their diversity? Many careful ecologists are not so sure. To explain their doubt, they point to two real phenomena—biotic reserves and diversity hot spots—and the hope associated with combining them.

Biotic reserves constitute a collection of relictual habitats scattered all over the world. They vary greatly in size, but all exist to preserve a remnant of a once vast network of Edens. As an ensemble, they are hyperdispersed in biotic space. That is to say, they form a deliberately varied collection. We spend our limited resources to save the dwindling last bits of long-leaf pine forest or tall-grass prairie or Arizona riparian bottomland. We delay reserving that which is presently common. Later, I will explain that this approach has indeed given us precious time, although it cannot forever avert the evil decree.

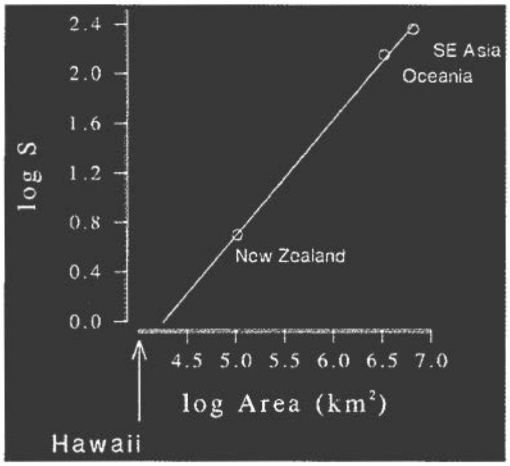

Fig. 3. The interprovincial species–area relationship for cerypachine and ponerine ants extrapolated to the area of a province that would sustain a single native species. That area is 18,354 km^2. Hawaii has only 10,378 km^2 and has no native species of these ants.

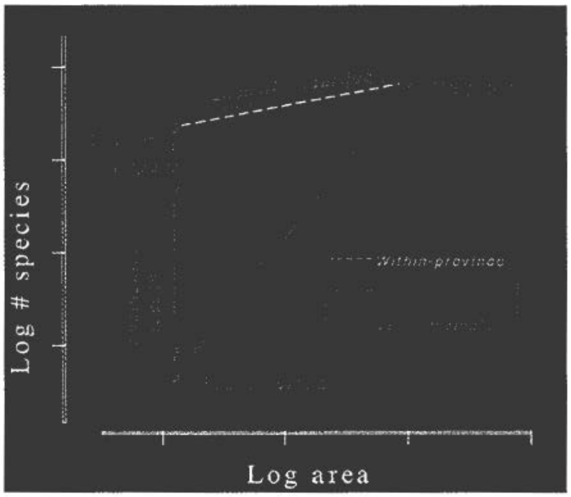

Fig. 4. The three phases of mass extinction that follow a severe reduction in area. Endemic extinctions occur because species lose all their habitat. Sink species disappear because all their source populations lose their habitats. Accidental extinctions remove species that suffer a run of bad luck despite being able to sustain their populations during an average generation.

What is the apparent significance of hot spots of diversity? They tantalize us with the promise that we can minimize the amount of reservation needed to prevent a mass extinction. For example, about 44% of all vascular plant species and 35% of all species of mammals, birds, reptiles, and amphibians live confined to only about 1.4% of its land in 25 hot spots (37). Clearly, this 1.4% is critical. If it goes, so do all those species. But, it is very tempting to reverse that argument: Let us save the 1.4%. Perhaps, then, we will save all those species now living in it. That is the combination of reservation and hot spots that offers hope to some conservation biologists.

Unfortunately, the interprovincial pattern of diversity questions that hope. It underscores the fact that diversity is the outcome of dynamical processes, whereas hot spots constitute a static view of diversity. The differences among the scales of species–area relationships and their z-values provide a dynamic basis for predicting what will happen to species diversity and to speciation in the future.

Following a reduction in province size, the three species–area relationships predict a mass extinction in three phases (Fig. 4). First, we lose the endemics—those species whose habitat gets entirely expropriated (40). These extinctions will be deterministic and virtually instantaneous. Second, we lose the sink species—those which get restricted to marginal habitats (i.e., habitats in which their death rates exceed their birth rates). These extinctions will also be deterministic (41, 42); however, they will take a while because some individuals of sink species not only survive, but may also reproduce. Third, we lose not particular species, but the diversity in excess of the new steady state. These extinctions will be stochastic, and predicting their rate—even their average rate to an order of magnitude—may not be possible as I will soon point out. Nevertheless, it is possible to say that the diversity lost because of these extinctions will be deterministically and irreplaceably lost—after all, the predicted loss constitutes however many species it takes to restore a steady-state diversity to the earth.

Stages I and II: The Deterministic Extinctions

The coefficients of species–area equations at smaller scales permit us to estimate the proportions of species that are endemics or sink species. The prediction that we lose the sum of these is the well known and often cited equation of island biogeography:

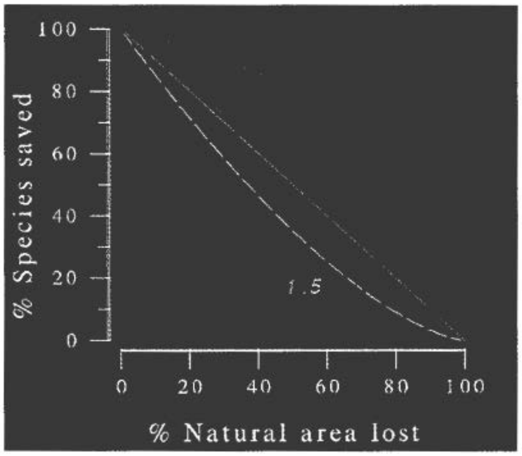

Fig. 5. Declining area reduces the proportion of species maintained at steady state. The amount of the reduction depends on the z-value. This figure shows the result for z-values of 1.5 (– – –), 1 (—), 0.9 (- · · · · -), and 0.3 (- - -). Assuming the latter, which is a typical archipelagic z, we would predict the least severe losses. But data show that interprovincial z-values are close to unity.

$$S = A^{0.3}$$

where S and A are proportions of diversity and natural area that remain. I plot this relationship in Fig. 5.

Some impatient types have complained that these predicted extinctions have not happened. In some cases, no doubt, their analyses have been flawed (43). But another factor has been at work. Conservation's two strategies have stayed the imposition of the island equation, and may even have reduced its severity. Focusing on preserving the habitats most likely to vanish entirely, we considerably reduced the likelihood that any species would lose everything, including its sink habitats. That transferred some extinction of endemics to the category of extinction of sink species. And, although the island equation assumes so, we have not lost natural area randomly. Instead, we diversified our biotic reserves, making them a stratified sample of our habitats and the species they harbor. Although we still have no analytical theory to predict the power coefficient of the island equation, a stratified sample has to have preserved more habitats and their species than a random sample would have. That is the good news.

Other news is more upsetting. Extinction, like speciation, is a dynamical process. Extinction, like speciation, takes time (44). Relaxation to island equilibrium is likely to take a number of human generations (see ref. 37 and references 34–43 therein).

We know that the past 10,000 years have not sufficed to allow mammals on newly formed islands to attain new steady states (e.g., Fig. 6). Lizard species diversity in the wheatbelt reserves of Western Australia has declined to a z-value of 0.26, but has yet to reach the value of 0.36 found among the state's true islands (Fig. 7). And on new islands in the Sea of Cortez, lizard species diversity continued to decline for at least 12,000 years (45). We must not be too impatient.

Stage III: The Stochastic Extinctions

A true island reaches its steady state as a result of the balance between immigration and extinction. But our shrunken natural world will see no immigrations. Species that become extinct cannot immigrate from the past to recolonize the world of the future. So, even after our new world reaches its levels of island-like diversity, its diversity will continue to diminish.

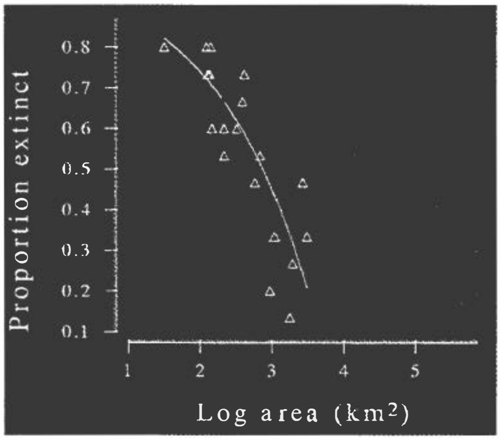

Fig. 6. Mammal diversity on Sunda Islands (circles) and southwestern U.S. mountaintops (triangles). These isolates formed about 10,000 years ago at the end of the Pleistocene. In both archipelagos, larger islands have experienced proportionately less extinction. After Rosenzweig's (1) figure 6.5.

Relaxation below the island-like steady state will come from inflated extinction rates. But the species of our shrunken island world will all begin with at least one source population. They will all have enough habitat to keep them going in perpetuity—provided that nothing ever changes in those habitats. But something always changes. So, species will vanish simply because they lose one roll of the dice. Global warming may push their remaining habitats out of all reserves and into cornfields or the sea (46). New parasites and diseases will appear to take their toll. A series of bad weather events may be too much for some dwindled populations.

The Depauperate Steady State

Accidents that eradicate successful species have always accompanied life. However, in ordinary times, life has replaced such losses by speciation. Not this time. This time the loss of area will have also depressed the speciation rate curve. Constricted geographic ranges will have fewer isolates. Many species will be restricted to a single reserve with no chance of further allopatric speciation. The loss of ecological theater will change the evolutionary play. New speciations will not be able to keep up with the losses.

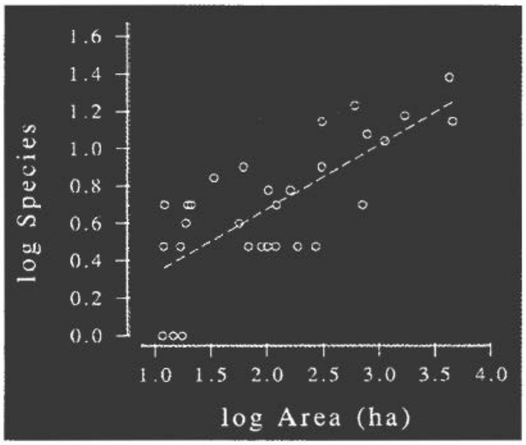

Fig. 7. Lizard species diversity in the 22 isolated reserves of Western Australia's wheatbelt (triangles) and its marine islands (circles). The reserve species area curve shows some decline from what would be expected in pre-European times as its z-value is 0.26. But it has not yet reached the value of 0.36 found among the true islands.

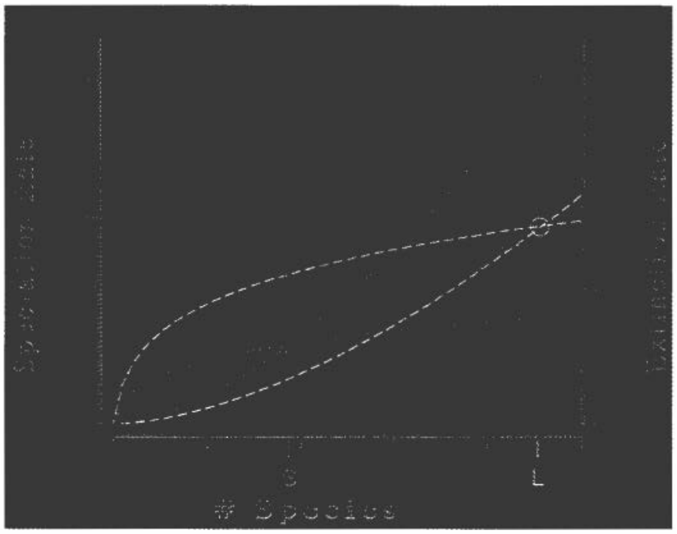

Fig. 8. Diversity dynamics of three provinces of different area: S (small, -····-); M (medium, —); and L (large, - - -). Extinction rates have positive second derivatives; speciation rates have negative second derivatives. The steady state of each province is indicated at the point where speciation and extinction balance (diamond, small; box, medium; circle, large).

Yes, eventually, a balance will be restored. But before that happens, the total extinction rate must decline to the level of the total speciation rate (Fig. 8). Thus, at the steady state of the future, when life is replacing its losses by speciation, it will not build back the diversity it now enjoys. The new balance will occur with life decimated of its richness.

Like any evolutionarily independent province, our future world must seek its steady state along the interprovincial species–area curve. The z-value of this curve is approximately unity, so our losses of species should be approximately linear (Fig. 5). Lose 10% of the natural world's surface and we save about 90% of its species. Lose 95% and save only 5% of the species. Diversity in provinces appears to have been following such a law for hundreds of millions of years. We have no evidence to indicate that law has been repealed.

This prediction is much more severe a decree than the usual proclamation of doom. The usual bad news predicts the loss of about half the world's species. But such rosy predictions rest on the z-value of island species–area curves, which is only about 0.3.

How long does it take to restore a steady state in species diversity? Perhaps a very long time—although, in truth, we do not know. One thing we can say. The process of re-achieving a steady state after this biotic crisis will not resemble any previous recovery from a mass extinction.

- First, as we have seen, life will not recover anything like its previous levels of diversity.
- Second, some taxa will vanish forever. The new world's area will fall below the threshold they require for any speciation (24), and so it will be unable to sustain even one of these species, just as Hawaii cannot sustain even one species of native insect that specializes in eating bracken, or even one ant of certain subfamilies (see above).
- Third, previous mass extinctions were a violent interruption and perturbation of steady-state diversities. Afterward, background conditions returned and life recovered its steady states through the action of speciation. In this case, however, the mass extinctions represent a gradual relaxation to a new steady state dictated by the shrunken area available to nature. Thus, recovery of steady-state dynamics will occur as soon as the mass extinction is over—i.e., after complete relaxation. The trajectory of extinctions—not the trajectory

of originations—will determine how long the process will take.

We can determine an upper limit to relaxation time by realizing that, as a dynamic process, its time scale should resemble its flux rates. Most of the time speciation–extinction flux is glacial. Estimates of background rates come from both the fossil record and modern phylogenetic reconstructions. Mammal species appear to turn over on a scale of 10^5 yr. Shelly marine invertebrates on a scale of 10^6 yr. But these are normal background rates.

Human pressure may greatly accelerate the relaxation process by increasing accidental extinction rates. Various human activities suggest this. We increasingly commingle evolutionarily separate provincial biotas, creating the New Pangaea and introducing native species to predatory and competitive threats from exotics (47). We rapidly transport novel diseases and parasites around the world. We simplify biotic temporal regimes (for example by limiting disturbances such as fire). And we are warming the globe. The National Research Council (44) implicates exotic species or lack of adequate disturbance as the root cause in endangering a significant proportion of threatened U.S. species. But global warming may constitute the worst threat of all: by altering the basic abiotic conditions of reserves, it can destroy their ability to do much of their job. When the earth was covered with contiguous tracts of natural habitat, species could track such changes, moving to keep up with the shifts in location of their favored habitats and so avoiding extinction (48–50). But today, with natural habitats restricted to patches of reserves, this is not possible. Meanwhile, we show little sign of abandoning the destruction of habitat that brings deterministic extinction to species.

So, how long could it take to achieve a world so poor in species that its speciation rates once again counterbalance its accidental extinctions? Perhaps a million years, perhaps a hundred.

Reconciliation Ecology

Not all species are losing ground to us. Some live with us and prosper. In German, they are known as *kulturfolger*—culture followers. One might dream that these *kulturfolger* would speciate rapidly and take up the slack. But the population isolates of *kulturfolger* cannot make much evolutionary headway. To do so would be to adapt to local circumstances, and that adaptation requires time. Thus, it requires that the isolates face some stability in the environmental challenges we cast at them. But Technological Man does not allow stable intervals; we constantly change our habitats and exert new pressures on the *kulturfolger*. They may not disappear, but they are also unlikely to radiate into a wide variety of new species.

Can we find a way to change all this? In the felicitous metaphor of Norman Myers, can we find a way to save Darwin's Genie and the treasures it has given us? We can. But not if we accept today's dominant strategy of conservation biology. For historical reasons, conservation biology has become mired in an attitude of confrontation: The green forces of nature versus the green forces of money. Conservation divides the world into pristine habitats and ruined habitats. It tries to save and restore the former while preventing further loss.

Let us ignore the fact that all of us must live in one world, accepting both its economic environment and its ecology. Let us also ignore the fact that if we view nature as an embattled victim, we are ultimately consigning her to defeat at the hands of the superior forces of human population pressure, human guile, and human greed. Let us instead concentrate on the science.

Science insists that area is an intrinsic property of natural ecosystems. To maintain their diversity, they must have their area. Thus, conservation biology has to address itself to the habitats in which human beings live, work, and play. Conservation biology has to learn how to share anthropogenic habitats with wild species. It needs to discover how to modify and diversify those habitats so that they harbor a wide variety of species. I call this sort of conservation biology reconciliation ecology.

Reconciliation ecology seeks techniques of management that turn more species into *kulturfolger*, giving them back their geographical ranges without taking away ours. It takes advantage of the fact that the earth remains as large as ever, but that we have devised new habitats in which most species cannot function at all. If we meet wild species half way, many will adapt to our world. They will spread in it and reestablish their potential for speciation and their resistance to extinction.

A growing number of examples demonstrates that reconciliation ecology can work. Countryside biogeography is showing that some styles of land use are already compatible with the needs of many species (51–53). Projects devoted to particular species are bringing them back in anthropogenic, economically productive habitats (54–56). Other projects focus on developing and managing habitats (57–60). The examples I cite are but a small sample of those I have collected over the past 3 years.

One project created a single patch of salt marsh at a critical point in the migratory flyway of perhaps a third of all of the bird individuals in Europe and western Asia. In doing so, it saved at least a fraction of the 257 species that use that flyway (61). Until 30 years ago, a nearby 12-km^2 natural salt marsh had done this job. But the natural salt marsh was totally destroyed by resort development. Today's patch of salt marsh little resembles its predecessor or any natural habitat. It is carefully built up, contoured, and planted on a refuse dump. And it is regularly irrigated with treated, nutrient-rich sewage water.

Another project set out to save a long-leaf pine forest and its endangered species such as the red-cockaded woodpecker (62). Through novel, carefully studied, and continuous management in a large, important Air Force base, it has multiplied—by two orders of magnitude—the area covered by a sustainable long-leaf pine forest. Meanwhile, residential, recreational, timbering, and all military uses continue. This is not restoration. Never before has there been a long-leaf pine forest like this one.

As the millennium changes, the media engorge on visions of the future. I have yet to hear one that does not involve technology. My own vision of the year 2100 is fundamentally different. We will have the technology, but we will be using it in magnificent surroundings that help to bring us peace and fulfillment, and to discharge our responsibilities to nature. I see my great-grandchildren opening their doors on a world of wonders.

Perhaps this vision is mere fantasy. Perhaps it is my way to cope with the unthinkable, because, indeed, the alternative is too disheartening to contemplate. Evidence indicates that we cannot preserve the large scale at the tiny scale (63). Area constitutes a basic inherent property of every biome, a property crucial to the dynamical functioning of its components. So it is an oxymoron to imagine a pristine biome that retains only 2 or 5 or even 10% of its original size.

In particular, area helps set the provincial diversity of a mature province. In turn, provincial diversity determines local diversity—local diversity can only echo provincial diversity. Thus, if the area available to native species remains very low or declines even farther, the loss of speciation rate will prevent even our biotic preserves from maintaining their diversities for very long.

For an evolutionary ecologist, the year 2100 lies in plain sight, a short trip into the future. At the end of this path, we could find a splendid set of human environments, clean and brimming with a richness of life that will invigorate and restore our spirits. But this will happen only if we take advantage of the ecological opportunities we still have.

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1. Rosenzweig, M. L. (1995) *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, U.K.).
2. Rosenzweig, M. L. & Ziv, Y. (1999) *Ecography* **22,** 614–628.
3. Mitton, J. B. (1997) *Selection in Natural Populations* (Oxford Univ. Press, Oxford).
4. Hanski, I. & Gilpin, M. E., eds. (1997) *Metapopulation Dynamics: Ecology, Genetics and Evolution* (Academic, New York).
5. Harrison, S. (1998) in *Biodiversity Dynamics: Turnover of Populations, Taxa, and Communities*, eds. McKinney, M. L. & Drake, J. A. (Columbia Univ. Press, New York).
6. Allen, J. C., Schaffer, W. M. & Rosko, D. J. (1993) *Nature (London)* **364,** 229–232.
7. Maurer, B. A. & Nott, M. P. (1998) in *Biodiversity Dynamics: Turnover of Populations, Taxa, and Communities,* eds. McKinney, M. L & Drake, J. A. (Columbia Univ. Press, New York), pp. 31–50.
8. Leigh, E. G. (1981) *J. Theor. Biol.* **90,** 213–239.
9. Goodman, D. (1987) in *Viable Populations for Conservation,* ed. Soule, M. E. (Cambridge Univ. Press, Cambridge, U.K.), pp. 11–34.
10. Gilpin, M. (1992) *J. Theor. Biol.* **154,** 1–8.
11. Lande, R. (1993) *Am. Nat.* **142,** 911–927.
12. Lynch, M., Conery, J. & Bürger, R. (1995) *Am. Nat.* **146,** 489–518.
13. Pimm, S. L., Jones, H. L. & Diamond, J. (1988) *Am. Nat.* **132,** 757–785.
14. Belovsky, G. E., Mellison, C., Larson, C. & van Zandt, P. A. (1999) *Science* **286,** 1175–1177.
15. Mayr, E. (1954) in *Evolution as a Process,* eds. Huxley, J. S., Hardy, A. C. & Ford, E. B. (Allen and Unwin, London), pp. 157–180.
16. Brown, W. L., Jr. (1957) *Q. Rev. Biol.* **32,** 247–277.
17. Walsh, J. B. (1995) *Genetics* **139,** 421–428.
18. Greenbaum, I. F., Baker, R. J. & Ramsey, P. R. (1978) *Evolution* **32,** 646–654.
19. Templeton, A. R., Robertson, R. J., Brisson, J. & Strasburg, J. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5426–5432.
20. Hansen, T. A. (1980) *Paleobiology* **6,** 193–207.
21. Jablonski, D. (1986) *Science* **231,** 129–133.
22. Jackson, J. B. C. (1974) *Am. Nat.* **108,** 541–560.
23. McKinney, M. L. (1997) in *The Biology of Rarity*, eds. Kunin, W. E. & Gaston, K. J. (Chapman & Hall, London), pp. 110–129.
24. Losos, J. B. (1996) *Philos. Trans. R. Soc. London B* **351,** 847–854.
25. Boucot, A. J. (1975) *Evolution and Extinction Rate Controls* (Elsevier Scientific Publications, Amsterdam).
26. Miller, A. I. & Foote, M. (1996) *Paleobiology* **22,** 304–309.
27. Alroy, J. (1998) in *Biodiversity Dynamics: Turnover of Populations, Taxa and Communities,* eds. McKinney, M. L. & Drake, J. A. (Columbia Univ. Press, New York), pp. 232–287.
28. Brett, C. E., Ivany, L. C. & Schopf, K. M. (1996) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **127,** 1–20.
29. Miller, A. I. (1998) *Science* **281,** 1157–1160.
30. Rosenzweig, M. L. (1998) in *Biodiversity Dynamics: Turnover of Populations, Taxa, and Communities*, eds. McKinney, M. L. & Drake, J. A. (Columbia Univ. Press, New York), pp. 311–348.
31. Rosenzweig, M. L. (1999) in *Advanced Theoretical Ecology: Principles and Applications*, ed. McGlade, J. (Blackwell Science, Oxford), Vol. 80, pp. 249–281.
32. Tiffney, B. H. & Niklas, K. J. (1990) in *Causes of Evolution: A Paleontological Perspective*, eds. Ross, R. M. & Allmon, W. P. (Univ. of Chicago Press, Chicago), pp. 76–102.
33. Wilson, E. O. (1961) *Am. Nat.* **95,** 169–193.
34. Wilson, E. O. & Taylor, R. W. (1967) *The Ants of Polynesia (Hymenoptera: Formicidae)* (Bernice P. Bishop Museum, Honolulu).
35. Lawton, J. H. (1984) in *Ecological Communities: Conceptual Issues and the Evidence*, eds. Strong, D. R., Simberloff, D. S., Abele, L. G. & Thistle, A. B. (Princeton Univ. Press, Princeton).
36. Lawton, J. (1999) *Oikos* **84,** 177–192.
37. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. (2000) *Nature (London)* **403,** 853–858.
38. Huston, M. (1993) *Science* **262,** 1676–1680.
39. Vitousek, P., Mooney, H., Lubchenco, J. & Melillo, J. (1997) *Science* **277,** 494–499.
40. Harte, J. & Kinzig, A. (1997) *Oikos* **80,** 417–427.
41. Patterson, B. D. (1990) *Oikos* **59,** 330–342.
42. Patterson, B. D. & Atmar, W. (2000) in *Isolated Vertebrate Communities in the Tropics; Proc. 4th Intern. Symp*., ed. Rheinwald, G., (Bonn. Zool. Monogr.), Vol. 46, pp. 93–108.
43. Brooks, T. M., Pimm, S. L. & Collar, N. J. (1997) *Conserv. Biol.* **11,** 382–394.
44. National Research Council (1995) *Science and the Endangered Species Act* (Natl. Acad. Press, Washington, DC).
45. Wilcox, B. A. (1978) *Science* **199,** 996–998.
46. Peters, R. L. & Darling, J. D. S. (1985) *Bioscience* **35,** 707–717.
47. Mooney, H. A. & Cleland, E. E. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5446–5451.
48. Brett, C. E. (1998) *Palaios* **13,** 241–262.
49. Coope, G. R. (1987) in *Organization of Communities Past and Present*, eds. Gee, J. H. R. & Giller, P. S. (Blackwell Scientific, Oxford), pp. 421–438.
50. Davis, M. B. (1983) in *Late-Quaternary Environments of the United States*, ed. Wright, H. E., Jr. (Univ. of Minnesota Press, Minneapolis), pp. 166–181.
51. Daily, G., Ehrlich, P. R. & Sánchez-Azofeifa, G. A. (2001) *Ecol. Appl.* **11,** 1–13.
52. Vandermeer, J. & Perfecto, I. (1995) *Breakfast of Biodiversity* (Food First, Oakland, CA).
53. Greenberg, R., Bichier, P. & Sterling, J. (1997) *Biol. Conserv.* **80,** 235–247.
54. Denton, J. S., Hitchings, S. P., Beebee, T. J. C. & Gent, A. (1997) *Conservation Biology* **11,** 1329–1338.
55. Gaby, R., McMahon, M. P., Mazzoti, F. J., Gillies, W. N. & Wilcox, J. R. (1985) *J. Herpetol.* **19,** 189–198.
56. Yosef, R. & Grubb, T. C., Jr. (1994) *Auk* **111,** 465–469.
57. Bormann, F. H., Balmori, D. & Geballe, G. T. (1993) *Redesigning the American Lawn* (Yale Univ. Press, New Haven, CT).
58. Esselink, H., Geertsma, M., Kuper, J., Hustings, F. & van Berkel, H. (1995) *Proc. West. Found. Vertebr. Zool.* **6,** 287–293.
59. Edwards, V. M. (1995) *Dealing in Diversity: America's Market for Nature Conservation* (Cambridge Univ. Press, Cambridge, U.K.).
60. Western, D. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5458–5465.
61. Cherrington, M. (1999) *Earthwatch* May/June, 39–47.
62. McWhite, R. W., Green, D. R., Petrick, C. J., Seiber, S. M. & Hardesty, J. L. (1993) *Natural Resources Management Plan, Eglin Air Force Base, Florida* (U.S. Dept. of the Air Force, Eglin Air Force Base, FL).
63. Harrison, S. & Bruna, E. (1999) *Ecography* **22,** 225–232.

What was natural in the coastal oceans?

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Humans transformed Western Atlantic coastal marine ecosystems before modern ecological investigations began. Paleoecological, archeological, and historical reconstructions demonstrate incredible losses of large vertebrates and oysters from the entire Atlantic coast. Untold millions of large fishes, sharks, sea turtles, and manatees were removed from the Caribbean in the 17th to 19th centuries. Recent collapses of reef corals and seagrasses are due ultimately to losses of these large consumers as much as to more recent changes in climate, eutrophication, or outbreaks of disease. Overfishing in the 19th century reduced vast beds of oysters in Chesapeake Bay and other estuaries to a few percent of pristine abundances and promoted eutrophication. Mechanized harvesting of bottom fishes like cod set off a series of trophic cascades that eliminated kelp forests and then brought them back again as fishers fished their way down food webs to small invertebrates. Lastly, but most pervasively, mechanized harvesting of the entire continental shelf decimated large, long-lived fishes and destroyed three-dimensional habitats built up by sessile corals, bryozoans, and sponges. The universal pattern of losses demonstrates that no coastal ecosystem is pristine and few wild fisheries are sustainable along the entire Western Atlantic coast. Reconstructions of ecosystems lost only a century or two ago demonstrate attainable goals of establishing large and effective marine reserves if society is willing to pay the costs. Historical reconstructions provide a new scientific framework for manipulative experiments at the ecosystem scale to explore the feasibility and benefits of protection of our living coastal resources.

The persistent myth of the oceans as wilderness blinded ecologists to the massive loss of marine ecological diversity caused by overfishing and human inputs from the land over the past centuries. Until the 1980s, coral reefs, kelp forests, and other coastal habitats were discussed in scientific journals and textbooks as "natural" or "pristine" communities with little or no reference to the pervasive absence of large vertebrates or the widespread effects of pollution. This is because our concept of what is natural today is based on personal experience at the expense of historical perspective. Thus, "natural" means the way things were when we first saw them or exploited them, and "unnatural" means all subsequent change (1, 2). As in Magritte's masterpiece, *La Condition Humaine*, we see the world through a model of our own creation that organizes and filters understanding (3). In the present context, that filter is the sum total of anthropogenic change that took place in the oceans before we were born.

Not all ecological change is anthropogenic, however. Natural conditions in the oceans fluctuate greatly and sometimes suddenly on time scales that extend for decades to millennia. Thus, the filter of individual experience has two components. Changes caused by humans are the signal and natural variability constitutes the noise that obscures the human footprint (4–6). An important example of the potential magnitude of natural change comes from annually layered sediments of the Santa Barbara Basin (7). Abundances of fish scales of anchovies and sardines preserved in these sediments fluctuate more than an order of magnitude and exhibit nine major collapses and subsequent recoveries over 1700 years. These data and shorter records of fish catches suggest population cycles of 50 to 70 years associated with alteration of warm and cold physical regimes (4, 8). These cycles exceed the longest instrumental temperature records for the region and greatly complicate management of fisheries. How can one determine a sustainable catch against a background of such extreme natural variation?

Conventional ecological data are clearly inadequate to measure the ecological impacts of fishing or any other long-term human disturbance (4, 5, 9). Most observational records are much too short, too poorly replicated, and too uncontrolled to encompass even a single cycle of natural environmental variation. For example, detailed ecological observations of reef corals began only in the 1930s. There are a few "before and after" comparisons of community composition between surveys conducted up to a century ago and the present (10). However, the longest quantitative time series comprises only a few small intertidal quadrats on one small island over 30 years (11), and the longest comparable subtidal records encompass less than 20 years (12). In both cases, the interval studied is much less than the generation times of most common coral species and the intervals between some kinds of major disturbances in coral reef environments (13). Several kelp forests and rocky intertidal communities have been surveyed for about 25 years over scales of several hectares, so that the data approximate or exceed generation times of most important species, but not the periodicity of major climatic cycles (5, 6). Ecological data for oyster reefs, seagrass meadows, level bottoms, and virtually all other marine communities have similar limitations (14–18).

Paleoecological, archeological, and historical data are the only means for extending ecological records back long enough to document the characteristic variability of marine ecosystems and the magnitude of earlier anthropogenic change. Here I review the transformation of five Western Atlantic coastal ecosystems over the past few centuries as a result of human exploitation and pollution. My goals are to demonstrate the extraordinary magnitude of ecological changes that have been largely forgotten and to show how awareness of these changes can benefit efforts for conservation and restoration of coastal ecosystems. My focus is on benthic communities because extreme overfishing of pelagic species such as Atlantic whales, tuna, salmon, and herring is well known (19, 20). Transformations of benthos are subtler and known only to a few specialists. I also focus on ecological extinction because the magnitude of ecological changes is not generally understood (1, 2, 5, 9), and documentation of actual extinctions of marine species is just beginning (21). More importantly, too great a focus on species detracts attention from the transformation and loss of habitats and collapse of natural ecosystems that drive the processes of extinction.

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Caribbean Coral Reefs

Coral reefs are the largest durable biological constructions on earth. Reefs determine the physical structure of coastlines and adjacent ecosystems, including seagrass beds and lagoons. Coral reefs are the most taxonomically diverse marine ecosystems and provide complex habitat for myriad sessile and mobile organisms (22, 23). Recent discoveries of numerous sibling species suggest diversity is even greater than already described (24).

Species composition of Caribbean coral communities was stable for at least 125 thousand years, until the collapse in the 1980s (25–29). Different environments were dominated by distinct species assemblages of the corals *Acropora*, *Montastrea*, *Diploria,* and a few other genera, and the composition of these assemblages was similar over tens of kilometers of coastline for tens of thousands of years. Within each habitat, community membership was more predictable than expected by random sampling of the habitat-specific species pool. Thus, there was a clear baseline of coral community composition that serves for comparison with today.

Western Atlantic reef corals suffered catastrophic mortality in the 1980s (30–34). Live coral abundance declined to 1–2% cover from values of 50% or more. Dominant framework species of *Acropora* and *Montastrea* were severely affected. Besides overall reduction in coral abundance there was a shift in life histories of surviving species (13, 31–33). Western Atlantic *Acropora* and *Montastrea* are long-lived and reproduce by mass spawning of gametes that are fertilized and develop in the water column. These taxa are being replaced by smaller, shorter-lived *Agaricia* and *Porites* with internal fertilization and direct development, presumably because of selection for shorter life cycles in a regime of increased human disturbance.

The principal cause of coral mortality was overgrowth by macroalgae that exploded in abundance after an unidentified pathogen caused mass mortality of the enormously abundant grazing sea urchin *Diadema antillarum* in 1983–1984 (33, 35, 36). Increasing frequency of coral disease and bleaching were also major factors (30, 37, 38). A likely explanation for the formerly great abundance of *Diadema* is overfishing of major fish predators on *Diadema* and of large herbivorous fishes that had competed with *Diadema* for algal food (refs. 33, 36, 39–41; Fig. 1).

Overfishing allowed *Diadema* to increase in abundance and compensate for loss of herbivorous fishes that ate macroalgae before overfishing began. Then, when *Diadema* died out there were no other large grazers remaining to consume the algae. A key question is when overfishing began (9). Jamaican and other Caribbean reefs were so severely overfished in the 19th century that northern salt cod were imported *en masse* to stave off human starvation (42, 43). This early overfishing distorted ecological perspective to the point that reef fishes are described in the best modern textbook as small "aquarium species" rarely greater than 20–30 cm long (44). Most species of reef fishes are indeed small like other animals (45), but this says nothing about size–frequency distributions of communities of reef fishes before overfishing (and ecological investigations) began. Indeed, several of the earliest European explorers of the Caribbean (46, 47) carefully described large-scale native and early colonial fisheries of sharks, groupers, and other large fishes that have rarely been seen by most ecologists. Remarkably, the same modern textbook does not mention these species.

The stage for the collapse of Caribbean reef corals was set by the loss of large fishes sometime in the 19th century (9). The first modern study of Caribbean coral reefs in the 1950s (48) described coral communities like those in the Pleistocene when humans were absent from the Americas (25, 49). Coral communities did not change noticeably until the epidemic mortality of *Diadema antillarum* in the 1980s because ecological redundancy of herbivores obscured the potential effects of the loss of large herbivorous fishes for well over a century (9, 33, 50). Macroalgae were not able to overgrow corals until the last major herbivore was lost from the system. Lapointe suggested that nutrient enrichment might have tipped the competitive balance of macroalgae over corals (51), but this seems unlikely (40, 52, 53).

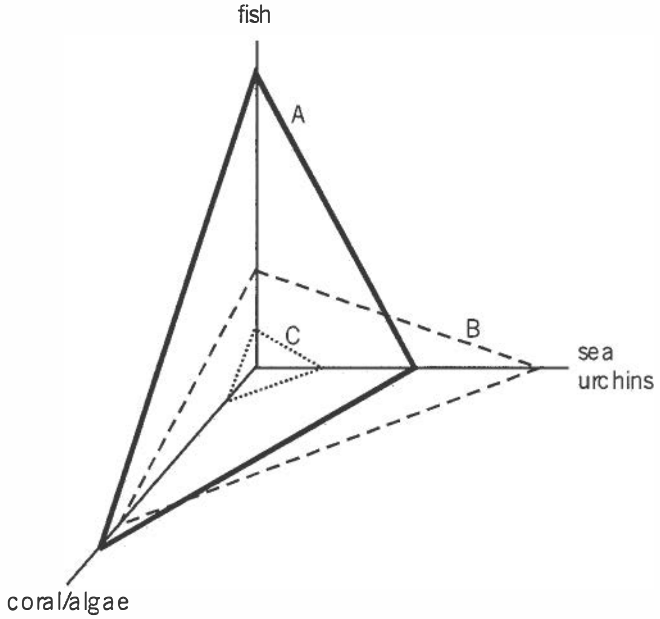

Fig. 1. Model of the consequences for reef corals of the increase in the sea urchin *Diadema antillarum* caused by overfishing of large predatory and herbivorous fishes and the subsequent mass mortality of *Diadema* caused by disease. Reproduced with permission from ref. 41 (Copyright 1994, The Royal Society). Plane A, pristine condition, with high ratio of corals to macroalgae because of intense grazing of macroalgae by fishes. Plane B, abundant *Diadema* grazed macroalgae formerly consumed by herbivorous fishes so the ratio of corals to macroalgae remained high despite intensive fishing. Plane C, mass mortality of *Diadema* caused by infectious disease allowed macroalgae to proliferate and overgrow corals.

In contrast to macroalgal overgrowth, outbreaks of coral disease are not understood (54). Climatic variability, humans as agents of dispersal of pathogens, habitat degradation, and pollutants have all been invoked as factors that favor increase of pathogens (55). However, there is no clear model or mechanism for how these factors could affect some species and not others, or consideration of the profound historical changes that previously affected reef ecosystems. Outbreaks of disease may be increasing because of the reduction of other species that once kept specific pathogens in check. In contrast, increasing frequency of severe episodes of coral bleaching is strongly correlated with high sea surface temperatures, and may truly reflect changes in global climate (56).

Caribbean Seagrass Meadows

Tropical American seagrasses are less diverse than corals, but seagrass meadows cover much greater areas than coral reefs (18, 57). Seagrasses enhance sediment stability, decrease wave energy, and increase water clarity as well as providing forage, habitat, and nurseries for diverse and abundant invertebrates and fishes (57, 58). The most common Caribbean species are turtle grass (*Thalassia testudinum*), manatee grass (*Syringodium filiforme*), and shoal grass (*Halodule wrightii*) (57). Seagrasses do not fossilize as readily as corals. However, well-preserved fossil assemblages of bivalve mollusks that inhabit the rhizome mat of seagrasses (59) suggest the persistence of seagrass communities throughout the Pleistocene. Seagrass beds were also persistent features on nautical charts.

Seagrasses along the Florida coast experienced mass mortality in the 1980s because of a wasting disease (60, 61). Mortality was positively density dependent and correlated with high temperatures and salinities, sulfide toxicity, self-shading, hypoxia, and infection by the slime mold *Labyrinthula* sp. Ecologists search for causes of seagrass mortality in terms of recent changes in hydrography and pollution (55, 61). However, all of the above factors except salinity and temperature have changed greatly because of massive exploitation centuries ago of sea turtles and manatees that gave the seagrasses their popular names.

Green turtles (*Chelonia mydas*) were extraordinarily abundant when Columbus arrived in the Caribbean (9, 62). Estimates of adult populations have been calculated, based on the assumption that population size was regulated by food limitation and by extrapolating from early hunting data from the Cayman Islands. Population sizes based on the carrying capacity of turtle grass range from 16 to 586 million 50-kg adults (62), whereas estimates based on early hunting data range from 33 to 39 million large nesting adults (9). Even the smallest estimate for green turtles exceeds the highest recorded wildebeest abundances in the Serengeti (63)!

What were the effects on seagrass beds of such enormous numbers of turtles? Blades of turtlegrass grow upward from the base and can reach 30 cm or more in length (57). Older, more distal portions are commonly heavily overgrown by microorganisms, fungi, algae, and invertebrates, and are broken off and transported *en masse* during storms (64). Green turtles crop turtlegrass 2–4 cm above the base, and individuals commonly return repeatedly to the same plots that are maintained by continuously cropping grazed areas to feed on more nutritious new shoots of the turtlegrass (64). When density of turtles is comparatively high, individual grazing plots may merge so that the entire turtlegrass bed is closely cropped (65). Such close cropping matches Dampier's (46) description of turtlegrass blades as "six Inches long" (15 cm) when turtles were abundant, in comparison with much greater lengths typically observed today (57). Grazing by green turtles also reduces 20-fold the flux of detritus and nitrogen to seagrass sediments and alters their microbial ecology (64, 66–68). This happens because turtles (*i*) consume more of the blades than fishes and invertebrates, (*ii*) metabolize cellulose of cell walls by microbial fermentation in their hindguts, and (*iii*) disperse feces and urine over large areas well away from seagrass beds. In contrast, fishes and invertebrates feeding on turtlegrass cannot metabolize the cellulose and do not migrate over such large areas (68).

Now consider the potential significance of the ecological demise of green turtles for turtlegrass in Florida Bay. Green turtles were formerly very abundant in South Florida (69), and all of the factors identified in seagrass die-offs except changes in temperature and salinity would have been profoundly altered by abundant green turtles. Concentration of sulfides in sediments increases with accumulation of organic material that may also cause anoxia within sediments and hypoxia of overlying waters (70), but green turtles greatly decrease accumulation of organic matter in sediments (68). Self-shading is due to the density and foliage height of the leaves, which also are greatly reduced by green turtles. Finally, infection by slime molds is positively correlated with density of turtlegrass (61) and probably depends on the amount of time senescing leaf tissues are exposed to the environment. Scientific descriptions of the sites of infections are vague, but leaf segments free of lesions caused by slime molds for use in experiments were always obtained from mid-to-basal sections of leaves (71), which are the youngest portions (57). In addition, infections illustrated in photographs occur along the distal portion of the blade (http://www.floridamarine.org/). Thus infection begins on those older portions of leaves that were typically grazed away when turtles were abundant. Elimination of green turtles is implicated on four counts as the ultimate factor in die-offs of turtlegrass; a hypothesis that could be tested by manipulative experiments of abundance of green turtles in turtlegrass beds on an appropriately massive scale.

The demise of green turtles is better documented (9, 69) than that of manatees (*Trichechus manatus*), which feed on manatee grass and other submerged vegetation (46, 72) and can metabolize cellulose as green turtles do (68). One- to two-ton manatees were sufficiently abundant along the low-lying and swampy coasts of Central America and northern South America to merit extensive and detailed descriptions of their natural history and how they were commonly hunted (46). Moreover, the much better documented and more recent demise of the dugong (*Dugong dugong*) in Australia suggests populations of these enormous relatives of the manatee of about 1 million along the Australian coast only a century ago (73). Dugongs plow through seagrass beds in Australia, reducing shoot density and biomass of by up to 90% (74). We will likely never know the equivalent ecological consequences of manatee grazing in pristine seagrass environments. However, once again Dampier (46) gives us a clue when he describes manatee grass as "7 or 8 Inches long" (20 cm) compared with lengths commonly exceeding 20 inches (50 cm) today (57).

Chesapeake Bay

Chesapeake Bay is the largest and historically most productive estuary in North America. During the 20th century, once very extensive meadows of seagrasses, oyster beds, clams, blue crabs, and fish declined precipitously, while abundance and production of phytoplankton, eutrophication, and episodes of hypoxia and anoxia correspondingly increased (75). Overfishing and increasing runoff of freshwater, nutrients, and sediment from the land seem the obvious culprits, but physical conditions are extremely variable (76) and hypoxia was first reported in the 1930s when modern ecological research was only just beginning (77, 78). Thus it is impossible to determine the extent of human influence solely on the basis of modern observations.

The stratigraphic record of sedimentation, pollen, seeds, diatoms, and geochemistry in sediment cores was used to reconstruct the ecological history of the northern half of the watershed over the past 2,000 years (75, 78–80). Environmental and biological fluctuations since European settlement exceed all earlier changes severalfold. Sedimentation rate and concentrations of organic carbon, sulfur, and ragweed pollen increased suddenly at the end of the 18th century. Diversity of diatom species, the ratio of benthic to planktonic diatoms, and the occurrence of seeds of benthic macrophytes gradually declined. Altogether, the results from the cores demonstrate an ecological shift in the upper Chesapeake Bay from predominantly benthic to predominantly planktonic primary production that was well under way by the early 19th century.

These results were corroborated by more recent observations of increasing phytoplankton biomass and decreasing submerged aquatic vegetation over the past 50–75 years (14, 81). Decline of the eelgrass *Zostera marina* was due primarily to wasting disease caused by the slime mold *Labyrinthula* sp., the same genus of pathogen affecting turtlegrass in Florida Bay (14, 82). Earliest reports of declines in eelgrass date from the 1890s, but mortality affecting >90% of eelgrass populations along the entire East Coast of North America occurred in the 1930s (14, 82).

Increase in phytoplankton was compounded by massive overfishing and physical destruction of oyster beds in the 19th century (15, 16, 77) in addition to increased loading of nutrients, especially nitrogen. Like seagrasses, oysters stabilize the substratum and provide complex habitat for hundreds of other species (16). Large oyster beds were a major hazard to navigation in bays and estuaries from New England to west

Florida until the mid-19th century, when large-scale mechanized harvesting began. Both the spatial extent of oyster beds and body size of individual oysters diminished greatly by the mid-19th century (15, 16). Numerous shell middens at least one quarter of a million cubic meters in volume attest to long history of aboriginal exploitation, but these great harvests were apparently sustainable. Shells in middens commonly exceed 30 cm, which agrees with colonial reports that oysters had to be cut in two to be eaten (16).

The filtration power of so many suspension-feeding animals must have been truly enormous (83). Calculations suggest that oysters before the 1870s filtered the equivalent of all of the water in Chesapeake Bay in less than 1 week, compared with 46 weeks for depleted modern stocks (84), a 50-fold difference! Subsequent model calculations suggest that this intense filtration would have reduced phytoplankton and zooplankton to a small fraction of present abundance regardless of increases in nutrients (85). These calculations are supported by striking reductions in abundance of phytoplankton after population explosions of introduced clams in lakes and estuaries (16).

Overfishing of oysters, decreased sediment stability, reduced benthic oxygen production because of loss of seagrasses, and increased nutrients from runoff acted synergistically to increase phytoplankton production at the expense of benthic resources and habitat. Increased eutrophication, frequency and scope of hypoxia, outbreaks of toxic microbes, and explosions of sea nettles and other noxious gelatinous zooplankton that feed on zooplankton and the larvae of invertebrates and fish are the result. Today Chesapeake Bay is a bacterially dominated ecosystem with a totally different trophic structure from a century ago (86). Similarly intense eutrophication occurs in other estuaries like Pamlico Sound (87), as well as along the continental shelf near the outflow of the Mississippi River (88). Oxygen deficiency is no longer restricted to bays and estuaries, but has spread to the open coastal ocean.

Kelps and Codfish in the Gulf of Maine

Kelp forests characterize large areas of warm temperate to subpolar coastal waters worldwide (89). Kelps provide complex habitat for a great diversity of fishes and invertebrates, including many commercially important species (89). Atlantic cod and other predatory ground fish were extremely abundant in kelp forests all along the coast of New England and eastern Canada until this century, but have now been fished to exhaustion (90). Loss of predatory fishes set off a series of complex ecological transformations that are still going on (90–92).

Large and abundant cod were fished from the Gulf of Maine for 5,000 years before the 19th century with no evidence of decline (92, 93). Cod remains constitute 80–90% of the bone mass in middens in Maine dating from 500 to 2,500 years ago. Vertebrae in middens suggest that cod commonly reached 1½ to 2 m in length, a size in accord with early European illustrations of drying cod the size of fishermen (19, 94). Large cod remained abundant until the 1920s, when mechanized trawling replaced traditional hook-and-line fishing. Cod abundance and size declined precipitously thereafter. Cod were virtually eliminated from coastal habitats in the 1980s and the average size of the few fishes caught was less than 30 to 40 cm. Today cod are so rare throughout the region that no cod were observed during hundreds of hours of underwater observations by diving and video cameras in the 1990s (90). Remaining fishes include small sculpins, skates, and dogfish, whereas cod has become ecologically extinct.

Elimination of cod and other large predatory ground fish resulted eventually in great increases in lobsters, crabs, sea urchins, and other invertebrate grazers and predators during the latter half of the 20th century (90–92). Lobsters had been fished down in size and abundance before mechanized fishing of cod, but subsequently increased in abundance with the elimination of coastal predators other than humans. Newly abundant sea urchins consumed all of the kelp, which was replaced by structurally "barren" substrata covered by encrusting coralline algae. Fishes and invertebrates dependent on kelps as habitat were also necessarily reduced. Subsequent "fishing down the food web" (95) of sea urchins beginning in 1987 resulted in rapid return of kelp forests, but without large populations of ground fishes. Humans are now the dominant predators in the Gulf of Maine coastal ecosystem. Hunting and fishing caused similar changes in kelp forests in Alaska and Southern California (5, 96, 97).

Benthic Communities on Continental Shelves

Direct and indirect effects of dredging and trawling on subtidal benthic communities have been reviewed extensively elsewhere (21, 98, 99). Most studies are from the North Sea and around the British Isles or from New Zealand and Australia, but similar effects are known from the Atlantic coasts of North America (99). Mechanized bottom fishing reduces abundance of echinoderms, mollusks, and worms by 10–90% each time the bottom is fished (98, 99), and the formerly abundant and long-lived skate *Raja laevis* has been trawled to ecological extinction (100). Most areas are dredged many times per year, thereby flattening the bottom (98, 99). Large sponges, bryozoans, corals, worms, or bivalves that provide important habitat for commercially important fishes and numerous smaller invertebrates are virtually eliminated (21, 98, 99). Large species that form these habitats grow so slowly that they cannot recover for decades to centuries.

Except for Northern Europe, intensive trawling and dredging on continental shelves began more recently than the overfishing described previously for other habitats (21, 98, 99). Nevertheless, few of the habitats affected were studied before mechanized fishing began, so that the quantitative effects of mechanized bottom fishing remain poorly documented in all but a few cases. The key point is that bottom fishing is already so intensive and pervasive that it is now effectively impossible to find "control" systems to help identify effects of fishing damage on natural communities. The only alternative to waiting decades or centuries for their recovery will be examination of changes in taxa from old museum collections and paleoecological analyses of Holocene shelf communities. Modern benthic communities already have been transformed beyond recognition on virtually the entire continental shelf of eastern North America.

Emerging Patterns

Five general patterns emerge from this brief review of Western Atlantic coastal ecosystems. The first three are well known from comparable effects of humans on terrestrial ecosystems. The last two patterns are less important in terrestrial environments because of differences in trophic levels harvested in the sea and on the land, and the insignificance of farming and absence of domesticated species in the oceans.

Vulnerability of Large Vertebrates. Large, long-lived vertebrates such as manatees, sea turtles, large fishes, and sharks were the first to disappear from coastal ecosystems in response to human activities because of their life history characteristics and large body size that attracted the most attention. Low fecundity, late maturation, and long generation times greatly reduce speed of recovery after harvesting or disease for all these organisms. Age of first reproduction for female manatees is about 6–10 years, after which they bear single offspring with a gestation period of about 1 year (72). Female sea turtles do not reach reproductive maturity for 7–30 years, after which they produce 1 to 7 clutches of ≈100–200 eggs every 1 to 3 years (101, 102). Moreover, these estimates of age of first reproduction are probably too young, and the true ages may range from as much as 40–60 years for some species (103).

Age (as opposed to size) of first reproduction for female groupers is poorly known but is only 6–7 years for the jewfish, which is the largest species (104), and numbers of eggs spawned are in the millions (104, 105). However, groupers reproduce in spawning aggregations that previously numbered in the tens to hundreds of thousands and occurred only at specific places and times of the year (105–107). As for sea turtles nesting on beaches, dense spawning aggregations make groupers easy to fish just at the time when they have the greatest potential to contribute to future generations (108).

Approximately 70% of living sharks and rays bear live young, and hammerheads exhibit placental viviparity (109, 110). Ages of maturation typically range from 6 to 18 years, but lemon sharks take 24 years. Gestation periods are long (6 to 22 months) and clutch sizes small (2 to 135). Thus, it is hardly surprising that sharks exhibit sudden collapse and slow recovery after relatively few years of intensive fishing (111, 112).

Collapse of Sessile Ecosystem Engineers. "Ecosystem engineers" are species that modify, maintain, or create habitats, thereby modulating availability of resources to other species (113). Reef-building corals, seagrasses, oysters, and kelps are among the most important ecosystem engineers in marine coastal environments. Their massive physical presence and three-dimensional complexity help stabilize the physical environment and provide habitat to thousands of generally smaller associated species (6, 22, 23, 50, 57, 58, 89, 91, 114). Once-vast populations of ecosystem engineers have now collapsed along the Western Atlantic coast from the southern Caribbean to the Gulf of Maine. The reasons range from complex shifts in competitive abilities of corals, seagrasses, and kelps after the removal of keystone consumer species or outbreaks of disease (refs. 18, 33, 61, 90–92; Fig. 1) to direct physical destruction of oyster beds and sponge–bryozoan gardens by mechanical dredging and trawling (15, 16, 98, 99, 114, 115).

Once, great coral reefs, seagrass meadows, and oyster reefs were products of growth of dominant framework species and accumulation of sediments and skeletal debris. Dead skeletons remain partially intact for various periods after the death of corals and oysters unless removed by mechanized harvesting, whereas sea grasses and kelps do not produce such durable remains, so that three-dimensionality rapidly disappears (90). Loss of habitat structure decreases growth and larval recruitment and increases mortality of engineering species (12, 31, 115). Diversity and abundance of associated species also drops precipitously (18, 116).

Time Lags Between Effects of Overfishing and Collapse of Ecosystem Engineers. Lengthy time lags between initial harvesting and many of the resulting ecological consequences are pervasive in tropical forests (117). Similarly in the coastal ocean, time lags of decades to centuries occurred between initial harvesting or destruction of large vertebrates and subsequent collapse of ecosystem engineers such as reef corals, seagrasses, or kelps (9, 33, 61, 90). Similar lags are apparent between increased fluxes of nutrients and sediments into coastal environments and collapse of reef corals (118), submerged macrophytes (14, 76), or oysters (15, 16, 85). Of course, oysters were intensively harvested by mining down the habitat, so their abundance declined much more rapidly than unfished corals and seagrasses.

One likely explanation for time lags is ecological redundancy, whereby other species take over the ecological role of species removed by harvesting. This is presumably what happened after overfishing on coral reefs (ref. 33; Fig. 1) and extirpation of green turtles in the Caribbean (9). Ecological redundancy should increase with taxonomic diversity, which may explain why time lags in the destruction of ecosystem engineers appear to decrease northward from corals and seagrasses in the Caribbean to kelps in the Gulf of Maine. Another important factor is widespread occurrence of threshold effects on human altered ecosystems (33, 119–122). These may involve simple thresholds in physiological tolerance to decreasing light or increasing sediments and nutrients, or more subtle density-dependent consequences of reduced abundance on fertilization, recruitment, or the ability to filter large volumes of water that reduces abundance of phytoplankton. Such negative feedbacks are exacerbated by the fact that both over-harvesting and increased nutrients and primary production work synergistically to reduce abundance of sessile ecosystem engineers (9, 76, 85, 114).

Fishing Down Food Webs. Top carnivores were never an important part of the human diet on land (123) but are the preferred large prey in the sea except for green turtles and sirenians. Smaller and smaller fishes, sea urchins, lobsters, and shrimps are replacing large fishes, turtles, and sharks as the remnant fisheries in all of the coastal ecosystems discussed herein (9, 33, 90, 95, 124). Free-living animals larger than 1 kg are increasingly rare and nearly absent on the reefs of Jamaica and many other sites throughout the Caribbean (33, 125). The process is reversible, but only by regulation of fishing.

Farming of the sea, or aquaculture, is a possible alternative to fishing, but one that carries its own set of potentially harmful consequences to coastal ecosystems, including eutrophication, pollution, and the spread of disease (126, 127). Cultured species include a wide diversity of algae, oysters, shrimps, and various fishes from mullets to salmon. Most of the problems of aquaculture of algae and herbivorous animals could be alleviated if goals were broadened to include ecosystem conservation and management, rather than only to produce food. For example, benthic algae could be farmed to remove excess nitrogen from the water column, and oysters and other suspension-feeding bivalves could be farmed to reduce algal blooms induced by eutrophication.

Rise of Microbes. Fishing down marine food webs and increasing pollution from the land are resulting in increasing abundance and widespread dominance of ecosystem processes by microbes. Eutrophication is most apparent in bays and estuaries like Chesapeake Bay (86), but it has extended onto the continental shelf (88). Outbreaks of previously rare or unreported toxic microbes and diseases are another example of the increasing importance of microbial disruption of coastal ecosystems (30, 35, 54, 55).

General Model of Coastal Ecosystem Collapse. I summarized much of the above in the simple qualitative model in Fig. 2 showing the demise of large animals and ecosystem engineers and the rise of microbes since European colonization of the Americas. The model is based on Western Atlantic case studies reviewed in this paper, but I predict the same general pattern will obtain for the entire global coastal ocean. The *y*-axes are logarithmic to capture the orders of magnitude changes in these variables. The time axis is deliberately general because onset of major changes depends more on timing of the onset of intensive harvesting or development of new fishing technologies than chronological age.

Early ecological extinction of large mobile animals defines the first major transition in the history of coastal marine ecosystems. Extirpation of large vertebrates preceded ecological investigations so that their absence has been uncritically accepted as the natural "baseline" condition. Their precipitous decline reflects greater economic desirability, ease of capture, and limited capacity for increase that is well documented for sea turtles, manatees, large fishes such as cod and groupers, and sharks. The

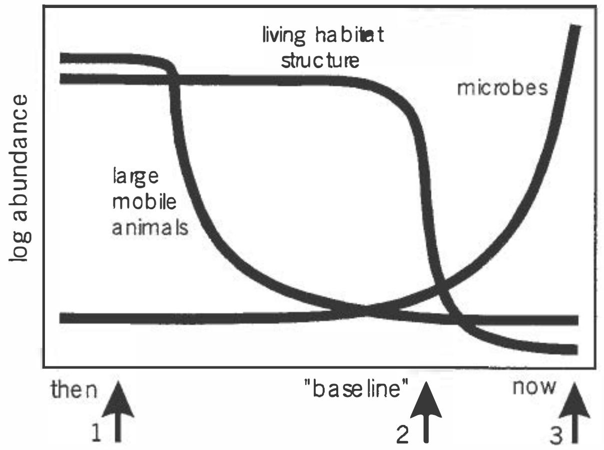

Fig. 2. Model of the collapse of Western Atlantic coastal ecosystems caused by overfishing. Arrows indicate the three major ecological transitions discussed in the text.

second major transformation reflects sudden collapse of sessile ecosystem engineers (reef corals, seagrasses, and kelps) caused by indirect effects of overfishing large vertebrates. Ecological dominance of microbes at the expense of macroorganisms (86) and increasing frequency of invasions of exotic species (128, 129) define the third major transition that is increasingly upon us (54, 55, 86, 88).

Why History Matters

Oceans are not wilderness and no Western Atlantic coastal habitat is pristine. The same is almost certainly true of coastal oceans worldwide, but this assertion needs rigorous documentation. Neotropical forests are greatly threatened by human activities and may disappear entirely within this century (117). The facts about tropical forests are widely known and much discussed by governments, international agencies, and the general public. By comparison, Neotropical coral reefs are already effectively "deforested" throughout their entire range, but this fact received almost no comparable attention until the 1990s (33, 130, 131). Moreover, human activities leading to the destruction of coral and oyster reefs, seagrass beds, or kelp forests began early in the 19th century or earlier, long before comprehensive scientific study began. In general, we are more aware of the mass extinction of large vertebrates at the end of the Pleistocene (123) than what happened in coastal seas only a century ago!

As in geology, the present is not always the key to the past, or to the future (132). Understanding what was natural is important not just for historical curiosity, but for rational management and conservation of coastal oceans in the future. I conclude with three basic points that emerge from comparisons of present conditions with historical baselines.

(*1*) No wild Atlantic coastal fishery is sustainable at anything close to present levels of exploitation. Coastal marine ecosystems already have been changed beyond recognition because of direct and indirect effects of overfishing. Most fishing is unsustainable because (*i*) inexorable growth of the human population drives increasing demand, (*ii*) development of mechanized fishing technologies severely damages the environment, (*iii*) cheap and rapid transportation makes even the most distant populations vulnerable to exploitation, and (*iv*) management has consistently failed to conserve depleted stocks (9, 15, 16, 33, 43, 77, 90, 98, 99). Evidence for ecological transformation and loss of fisheries resources on Western Atlantic coral reefs, seagrass beds, bays, estuaries, and the continental shelves is scientifically sound, and the burden of proof belongs on those who would still fish rather than the other way around (133). Monitoring is a basic tool for management, but no more monitoring is required to know what we have lost. Scientific efforts should be redirected toward evaluating options for restoration of resources rather than perpetuating the myth of sustainable fisheries. It is hard to imagine how increasingly sophisticated and frequent environmental monitoring and micromanagement could do a fraction of the good of simply stopping fishing. There is no rational *scientific* basis to continue fishing of wild stocks along the Atlantic coast of North America or in the Caribbean for the foreseeable future.

(*2*) Paleoecological, archeological, and historical reconstructions of coastal marine ecosystems provide the best evidence for predicting ecological consequences of establishing very large-scale marine reserves and other forms of rigorous protection of fisheries. Formerly pristine conditions of seagrass beds and oyster reefs of Chesapeake Bay (14–16), or of Caribbean coral reefs and seagrass beds and the hordes of large animals that lived upon them (9), seem fantastic and unbelievable today. Scientists, as well as the general public, set goals and expectations for marine reserves that are too low because they cannot imagine how coastal ecosystems used to be only a century ago (1, 2). These great changes, and frequently nonlinear transformations among alternative ecosystem states (31, 33, 119–122), make it almost impossible to predict the outcomes of complete protection from fishing and terrestrial inputs based on recent observations alone. Fortunately, historical records tell us what is possible. Because few of the large apex predators and herbivores are extinct, we could restore coastal resources for ecosystem services and managed harvest.

(*3*) Knowing the former abundance of large animals and ecosystem engineers makes it possible to design experiments to estimate per capita interaction strengths of ecologically extinct species (134, 135). The importance of such studies as a complement to results of human exclusion experiments (136) cannot be overestimated. Even among dedicated advocates, discussions of potential benefits of marine reserves rarely mention swordfish, sharks, sea turtles, or manatees (137), because almost no scientists have ever seen these animals in abundance or contemplated their restoration (1, 2, 9). Large mammals are considered in management plans for the Pacific Northwest because effects of protected sea otters, gray whales, and walrus on benthic communities are well known (96, 138). Most of the time, however, scientific debate revolves around species far down the original food webs, and former top predators and grazers are forgotten or ignored.

But to ignore these large animals is to give up most of what is attainable before we start. Very-large-scale experiments (enclosures of hundreds of hectares) with surviving large green turtles could be carried out in Florida Bay, for example, to determine how their presence affects mass wasting of seagrasses and losses of associated species (60, 61). Even such enormous experiments would probably cost less than increasingly sophisticated monitoring we are doing in so many places for want of a better idea (139). The same would be true for extensive reseeding followed by total protection of oyster beds in entire sections of bays and estuaries, or in entire embayments for cod. It is time scientists began an aggressive series of experiments involving large keystone species on the largest possible spatial and temporal scales. The alternative is absolute microbial domination of coastal ecosystems in 20 to 30 years. Is that the future of evolution in the oceans?

Much of this paper was the basis for a proposal to the National Center for Ecological Analysis and Synthesis (NCEAS) to reconstruct the human footprint on coastal marine ecosystems. I thank the members of the resulting NCEAS Marine Records Working Group for excellent discussion and criticism. Suggestions by Michael Graham, Michael Kirby, Nancy Knowlton, Hunter Lenihan, Pete Peterson, and Enric Sala greatly improved the manuscript. To all I am very grateful.

1. Pauly, D. (1995) *Trends Ecol. Evol.* **10,** 430.
2. Sheppard, C. (1995) *Mar. Poll. Bull.* **30,** 766–767.
3. Schama, S. (1995) *Landscape and Memory* (Knopf, New York).
4. McCall, A. D. (1996) *Calif. Coop. Fish. Invest.* **37,** 100–110.
5. Dayton, P. K., Tegner, M. J., Edwards, P. B. & Riser, K. L. (1998) *Ecol. Appl.* **8,** 309–322.
6. Dayton, P. K., Tegner, M. J., Edwards, P. B. & Riser, K. L. (1999) *Ecol. Monogr.* **69,** 219–250.
7. Baumgartner, T. R., Soutar, A. & Frerreira-Bartrina, V. (1992) *Calif. Coop. Fish. Invest.* **33,** 24–40.
8. Anderson, P. J. & Piatt, J. F. (1999) *Mar. Ecol. Prog. Ser.* **189,** 117–123.
9. Jackson, J. B. C. (1997) *Coral Reefs* **16,** S23–S32.
10. Davis, G. E. (1982) *Bull. Mar. Sci.* **32,** 608–623.
11. Connell, J. H., Hughes, T. P. & Wallace, C. C. (1997) *Ecol. Monogr.* **67,** 461–488.
12. Hughes, T. P. & Tanner, J. E. (2000) *Ecology* **81,** 2250–2263.
13. Jackson, J. B. C. (1991) *BioScience* **41,** 475–482.
14. Orth, R. J. & Moore, K. A. (1984) *Estuaries* **7,** 531–540.
15. Rothschild, B. J., Ault, J. S., Goulletquer, P. & Heral, M. (1994) *Mar. Ecol. Prog. Ser.* **111,** 29–39.
16. Kennedy, V. S. (1996) *J. Shellfish Res.* **15,** 177–183.
17. Hall, M. O., Durako, M. J., Fourqurean, J. W. & Zieman, J. C. (1999) *Estuaries* **22,** 445–459.
18. Fourqurean, J. W. & Robblee, M. B. (1999) *Estuaries* **22,** 345–357.
19. Cushing, D. H. (1988) *The Provident Sea* (Cambridge Univ. Press, Cambridge, U.K.).
20. Botsford, L. W., Castilla, J. C. & Peterson, C. H. (1997) *Science* **277,** 509–515.
21. Carlton, J. T., Geller, J. B., Reaka-Kudla, M. L. & Norse, E. A. (1999) *Annu. Rev. Ecol. Syst.* **30,** 515–538.
22. Paulay, G. (1997) in *Life and Death of Coral Reefs*, ed. Birkeland, C. (Chapman & Hall, New York), pp. 298–353.
23. Reaka-Kudla, M. L. (1997) in *Biodiversity II*, eds. Reaka-Kudla, M. L., Wilson, D. E. & Wilson, E. O. (Joseph Henry Press, Washington, DC), pp. 83–108.
24. Knowlton, N. & Jackson, J. B. C. (1994) *Trends Ecol. Evol.* **9,** 7–9.
25. Jackson, J. B. C. (1992) *Am. Zool.* **32,** 719–731.
26. Pandolfi, J. M. & Jackson, J. B. C. (1997) in *Proceedings of the Eighth International Coral Reef Symposium,* eds. Lessios, H. A. & Macintyre, I. G. (Smithsonian Tropical Research Institute, Balboa, Panama), Vol. 1, pp. 397–404.
27. Pandolfi, J. M. & Jackson, J. B. C. (2001) *Ecol. Monogr.* **71,** 49–67.
28. Aronson, R. B., Precht, W. F. & Macintyre, I. G. (1998) *Coral Reefs* **17,** 223–230.
29. Greenstein, B. J., Curran, H. A. & Pandolfi, J. M. (1998) *Coral Reefs* **17,** 249–261.
30. Gladfelter, W. B. (1982) *Bull. Mar. Sci.* **32,** 639–643.
31. Knowlton, N., Lang, J. C. & Keller, B. D. (1990) *Smithson. Contr. Mar. Sci.* **31,** 1–25.
32. Guzmán, H. M., Jackson, J. B. C. & Weil, E. (1991) *Coral Reefs* **10,** 1–12.
33. Hughes, T. P. (1994) *Science* **265,** 1547–1551.
34. Bak, R. P. M. & Nieuwland, G. (1995) *Bull. Mar. Sci.* **56,** 609–619.
35. Lessios, H. A., Robertson, D. R. & Cubit, J. D. (1984) *Science* **226,** 335–337.
36. Lessios, H. A. (1988) *Annu. Rev. Ecol. Syst.* **19,** 371–393.
37. McClanahan, T. R. & Muthiga, N. A. (1998) *Environ. Conserv.* **25,** 12–130.
38. Aronson, R. B. & Precht, W. F. (2000) *Hydrobiologia,* 1–14.
39. Hay, M. E. (1984) *Ecology* **65,** 446–454.
40. Lewis, S. M. (1986) *Ecol. Monogr.* **56,** 183–200.
41. Jackson, J. B. C. (1994) *Proc. Roy. Soc. London Ser. B* **344,** 55–60.
42. Duerden, J. E. (1901) *J. Imp. Agric. Dept. W. Indies*, 121–141.
43. Thompson, E. F. (1945) *Development and Welfare in the West Indies, Bulletin* 18 (Bridgetown, Barbados).
44. Sale, P. F. (1991) in *The Ecology of Fishes on Coral Reefs*, ed. Sale, P. F. (Academic, San Diego), pp. 3–15.
45. Brown, J. H. (1995) *Macroecology* (Univ. of Chicago Press, Chicago).
46. Dampier, W. (1729) *A New Voyage Around the World* (James and John Knapton, London); reprinted (1968) (Dover, New York).
47. de Oviedo, G. F. (1535–1557) *Historia General y Natural de las Indias, Islas y Tierra-Firme del Mar Oceano*; reprinted (1959) (Atlas, Madrid).
48. Goreau, T. F. (1959) *Ecology* **40,** 67–89.
49. Mesolella, K. J. (1967) *Science* **156,** 638–640.
50. Done, T. J., Ogden, J. C., Wiebe, W. J. & Rosen, B. R. (1996) in *Functional Roles of Biodiversity: A Global Perspective*, eds. Mooney, H. A., Cushman, J. H., Medina, E., Sala, O. E. & Schulze, E.-D. (Wiley, London), pp. 393–429.
51. Lapointe, B. E. (1997) *Limnol. Oceanogr.* **42,** 1119–1131.
52. Hughes, T. P., Szmant, A. M., Steneck, R., Carpenter, R. & Miller, S. (1999) *Limnol. Oceanogr.* **44,** 1583–1586.
53. Miller, M. W., Hay, M. E., Miller, S. L., Malone, D., Sotka, E. E. & Szmant, A. M. (1999) *Limnol. Oceanogr.* **44,** 1847–1861.
54. Richardson, L. L. (1998) *Trends Ecol. Evol.* **13,** 438–443.
55. Harvell, C. D., Kim, K., Burkholder, J. M., Colwell, R. R., Epstein, P. R., Grimes, D. J., Hofman, E. E., Lipp, E. K., Osterhaus, A. D. M. E., Overstreet, R. M., *et al.* (1999) *Science* **285,** 1505–1510.
56. Aronson, R. B., Precht, W. F., Macintyre, I. G. & Murdoch, T. J. T. (2000) *Nature (London)* **405,** 36.
57. Zieman, J. C. (1982) *The Ecology of the Seagrasses of South Florida: A Community Profile* (U.S. Fish and Wildlife Service, Office of Biological Services, Washington, DC).
58. Orth, R. J., Heck, K. L., Jr., & van Montfrans, J. (1984) *Estuaries* **7,** 339–350.
59. Jackson, J. B. C. (1972) *Bull. Mar. Sci.* **23,** 313–350.
60. Robblee, M. B., Barber, T. R., Carlson, P. R., Jr., Durako, M. J., Fourqurean, J. W., Muehlstein, L. K., Porter, D., Yarbro, L. A., Zieman, R. T. & Zieman, J. C. (1991) *Mar. Ecol. Prog. Ser.* **71,** 297–299.
61. Zieman, J. C., Fourqurean, J. W. & Frankovich, T. A. (1999) *Estuaries* **22,** 460–470.
62. Bjorndal, K. A., Bolten, A. B. & Chaloupka, M. Y. (2000) *Ecol. Appl.* **10,** 269–282.
63. Mduma, S. A. R, Sinclair, A. R. E. & Hilborn, R. (1999) *J. Anim. Ecol.* **68,** 1101–1122.
64. Ogden, J. C. (1980) in *Handbook of Seagrass Biology: An Ecosystem Perspective*, eds. Phillips, R. C. & McRoy, C. P. (Garland, New York), pp. 173–198.
65. Williams, S. L. (1988) *Mar. Biol.* **98,** 447–455.
66. Ogden, J. C., Robinson, L., Whitlock, H., Daganhart, H. & Cebula, R. (1983) *J. Exp. Mar. Biol. Ecol.* **66,** 199–205.
67. Thayer, G. W., Engel, D. W. & Bjorndal, K. A. (1982) *J. Exp. Mar. Biol. Ecol.* **62,** 173–183.
68. Thayer, G. W., Bjorndal, K. A., Ogden, J. C., Williams, S. L. & Zieman, J. C. (1984) *Estuaries* **7,** 351–376.
69. King, F. W. (1982) in *Biology and Conservation of Sea Turtles*, ed. Bjorndal, K. (Smithsonian Inst. Press, Washington, DC), pp. 183–188.
70. Carlson, P. R., Yarbro, L. A. & Barber, T. A. (1994) *Bull. Mar. Sci.* **54,** 733–746.
71. Durako, M. J. & Kuss, K. M. (1994) *Bull. Mar. Sci.* **54,** 727–732.
72. Reynolds, J. E., III, & Odell, D. K. (1991) *Manatees and Dugongs* (Facts On File, New York).
73. Lanyon, J. M., Limpus, C. J. & Marsh, H. (1989) in *Biology of Seagrasses: A Treatise on the Biology of Seagrasses with Special Reference to the Australian Region*, eds. Larkum, A. W. D., McComb, A. J. & Shepherd, S. A. (Elsevier, Amsterdam), pp. 610–634.
74. Preen, A. (1995) *Mar. Ecol. Prog. Ser.* **124,** 201–213.
75. Brush, G. S. (1994) in *The Changing Global Environment*, ed. Roberts, N. (Blackwell, Oxford), pp. 398–416.
76. Cronin, T., Willard, D., Karlsen, A., Ishman, S., Verardo, S., McGeehin, J., Kerhin, R., Holmes, C., Colman, S. & Zimmerman, A. (2000) *Geology* **28,** 3–6.
77. Wharton, J. (1957) *The Bounty of the Chesapeake* (Virginia Anniversary Celebration Corp.), Jamestown 390th Anniversary Historical Booklet 13.
78. Cooper, S. R. & Brush, G. S. (1991) *Science* **254,** 992–996.
79. Cooper, S. R. & Brush, G. S. (1993) *Estuaries* **16,** 617–626.
80. Cooper, S. R. (1995) *Ecol. Appl.* **5,** 703–723.
81. Harding, L. W., Jr., & Perry, E. S. (1997) *Mar. Ecol. Prog. Ser.* **157,** 39–52.
82. Muehlstein, L. K. (1989) *Dis. Aquat. Organ.* **7,** 211–221.
83. Officer, C. B., Smayda, T. J. & Mann, R. (1982) *Mar. Ecol. Prog. Ser.* **9,** 203–210.
84. Newell, R. I. E. (1988) in *Understanding the Estuary: Advances in Chesapeake Bay Research*, eds. Lynch, M. P. & Krome, E. C. (Chesapeake Research Consortium 129, CBP/TRS 24/88).
85. Ulanowicz, R. E. & Tuttle, J. H. (1992) *Estuaries* **15,** 298–306.
86. Jonas, R. B. (1997) *Am. Zool.* **37,** 612–620.
87. Paerl, H. W., Pinckney, J. L., Fear, J. M. & Peierls, B. L. (1998) *Mar. Ecol. Prog. Ser.* **166,** 17–25.
88. Turner, R. E. & Rabalais, N. N. (1994) *Nature (London)* **368,** 619–621.
89. Mann, K. H. (1982) *Ecology of Coastal Waters: A Systems Approach* (Univ. of California Press, Berkeley).
90. Steneck, R. S. (1997) in *Proceedings of the Gulf of Maine Ecosystem Dynamics Scientific Symposium and Workshop*, RARGOM Report 91-1, eds. Wallace, G. T. & Braasch, E. F. (Regional Association for Research on the Gulf of Maine, Hanover, NH), pp. 151–165.
91. Elner, R. W. & Vadas, R. L. (1990) *Am. Nat.* **136,** 108–125.
92. Witman, J. D. & Sebens, K. P. (1992) *Oecologia* **90,** 305–315.
93. Bourque, B. J. (1995) *Diversity and Complexity in Prehistoric Maritime Societies: A Gulf of Maine Perspective* (Plenum, New York).
94. de la Morandière, C. (1962–1966) *Histoire de la Pêche Française de la Morue dans l'Amérique Septentrionale* (Maisonneuve and Larose, Paris), Vols. 1–3.
95. Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F., Jr. (1998) *Science* **279,** 860–863.
96. Simenstad, C. A., Estes, J. A. & Kenyon, K. W. (1978) *Science* **200,** 403–411.
97. Estes, J. A., Duggins, D. O. & Rathburn, G. B. (1989) *Conserv. Biol.* **3,** 252–264.
98. Dayton, P. K, Thrush, S. F., Agardy, M. T. & Hofman, R. J. (1995) *Aquat. Conserv. Mar. Freshwater Ecosyst.* **5,** 205–232.

99. Watling, L. & Norse, E. A. (1998) *Conserv. Biol.* **12,** 1180–1197.
100. Casey, J. M. & Myers, R. A. (1998) *Science* **281,** 690–692.
101. Committee on Sea Turtle Conservation, National Research Council (1990) *Decline of the Sea Turtles: Causes and Prevention* (Natl. Acad. Press, Washington, DC).
102. Von Buskirk, J. (1994) *Copeia* **1994,** 66–81.
103. Bjorndal, K. A. & Zug, G. R. (1995) in *Biology and Conservation of Sea Turtles*, ed. Bjorndal, K. A. (Smithsonian Inst. Press, Washington, DC), 2nd. Ed., pp. 599–600.
104. Bullock, L. H., Murphy, M. D., Godcharles, M. F. & Mitchell, M. E. (1992) *Fish. Bull.* **90,** 243–249.
105. Carter, J., Marrow, G. J. & Pryor, V. (1990) *Proc. Gulf Caribb. Fish. Inst.* **43,** 65–111.
106. Sadovy, Y. (1990) *Proc. Gulf Caribb. Fish. Inst.* **43,** 43–64.
107. Smith, C. L. (1972) *Trans. Am. Fish. Soc.* **101,** 257–261.
108. Johannes, R. E. (1976) *Words of the Lagoon* (Univ. of California Press, Berkeley).
109. Branstetter, S. (1990) in *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries*, eds. Pratt, H. L., Jr., Gruber, S. H. & Taniuchi, T. (U.S. Dept. of Commerce, Washington, DC), NOAA Technical Report NMFS 90, pp. 17–28.
110. Pratt, H. L., Jr., & Casey, J. G. (1990) in *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries*, eds. Pratt, H. L., Jr., Gruber, S. H. & Taniuchi, T. (U.S. Dept. of Commerce, Washington, DC), NOAA Technical Report NMFS 90, pp. 97–109.
111. Compagno, L. J. V. (1990) in *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries,* eds. Pratt, H. L., Jr., Gruber, S. H. & Taniuchi, T. (U.S. Dept. of Commerce, Washington, DC), NOAA Technical Report NMFS 90, pp. 391–414.
112. Anderson, E. D. (1990) in *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries*, eds. Pratt, H. L., Jr., Gruber, S. H. & Taniuchi, T. (U.S. Dept. of Commerce, Washington, DC), NOAA Technical Report NMFS 90, pp. 473–484.
113. Jones, C. G., Lawton, J. H. & Shachak, M. (1994) *Oikos* **69,** 373–386.
114. Lenihan, H. S. & Peterson, C. H. (1998) *Ecol. Appl.* **8,** 128–140.
115. Lenihan, H. S. (1999) *Ecol. Monogr.* **69,** 251–275.
116. Lenihan, H. S., Peterson, C. H., Byers, J. E., Grabowski, J. H., Thayer, G. W. & Colby, D. R. (2001) *Ecol. Appl.*, in press.
117. Terborgh, J. (1999) *Requiem for Nature* (Island Press, Washington, DC).
118. Lewis, J. B. (1984) *Coral Reefs* **3,** 117–122.
119. Sutherland, J. P. (1974) *Am. Nat.* **108,** 859–873.
120. Peterson, C. H. (1984) *Am. Nat.* **124,** 127–133.
121. Knowlton, N. (1992) *Am. Zool.* **32,** 674–682.
122. Paine, R. T., Tegner, M. J. & Johnson, E. A. (1998) *Ecosystems* **1,** 535–545.
123. Diamond, J. (1997) *Guns, Germs and Steel: The Fates of Human Societies* (Norton, New York).
124. Steneck, R. S. (1998) *Trends Ecol. Evol.* **13,** 429–430.
125. Munro, J. L. (1983) *ICLARM Study Rev.* **7,** 1–276.
126. Svennevig, N., Reinertsen, H. & New, M., eds. (1999) *Sustainable Aquaculture: Food for the Future?* (Balkema, Rotterdam, The Netherlands).
127. Naylor, R. L., Goldburg, R. J., Primavera, J. H., Kaufsky, N., Beveredge, M. C. M., Clay, J., Folke, C., Lubchenco, J., Mooney, H. & Troell, M. (2000) *Nature (London)* **405,** 1017–1024.
128. Carlton, J. T. (1989) *Conserv. Biol.* **3,** 265–273.
129. Meinesz, A. (1999) *Killer Algae* (Univ. of Chicago Press, Chicago).
130. Wilkinson, C. R. (1992) in *Proceedings of the Seventh International Coral Reef Symposium,* ed. Richmond, R. (Univ. of Guam Press, Mangilao, Guam), Vol. 1, pp. 11–21.
131. Ginsburg, R. N., compiler (1994) *Proceedings of the Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History* 1993 (Rosenstiel School of Marine and Atmospheric Science, Univ. of Miami, Miami).
132. Ager, D. (1993) *The New Catastrophism* (Cambridge Univ. Press, Cambridge, U.K.).
133. Dayton, P. K. (1998) *Science* **279,** 821–822.
134. Paine, R. T. (1992) *Nature (London)* **355,** 73–75.
135. Wootton, J. T. (1997) *Ecol. Monogr.* **67,** 45–64.
136. Castilla, J. C. (1999) *Trends Ecol. Ecol.* **14,** 280–283.
137. Murray, S. N., Ambrose, R. F., Bohnsack, J. A., Botsford, L. W., Carr, M. H., Davis, G. E., Dayton, P. K., Gotshall, D., Gunderson, D. R., Hixon, M. A., *et al.* (1999) *Fisheries* **24,** 11–25.
138. Bowen, W. D. (1997) *Mar. Ecol. Prog. Ser.* **158,** 267–274.
139. Boesch, D. F. (2000) *Env. Res. Sect. A* **82,** 134–142.

The future of coral reefs

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Coral reefs, with their millions of species, have changed profoundly because of the effects of people, and will continue to do so for the foreseeable future. Reefs are subject to many of the same processes that affect other human-dominated ecosystems, but some special features merit emphasis: (*i*) Many dominant reef builders spawn eggs and sperm into the water column, where fertilization occurs. They are thus particularly vulnerable to Allee effects, including potential extinction associated with chronic reproductive failure. (*ii*) The corals likely to be most resistant to the effects of habitat degradation are small, short-lived "weedy" corals that have limited dispersal capabilities at the larval stage. Habitat degradation, together with habitat fragmentation, will therefore lead to the establishment of genetically isolated clusters of inbreeding corals. (*iii*) Increases in average sea temperatures by as little as 1°C, a likely result of global climate change, can cause coral "bleaching" (the breakdown of coral–algal symbiosis), changes in symbiont communities, and coral death. (*iv*) The activities of people near reefs increase both fishing pressure and nutrient inputs. In general, these processes favor more rapidly growing competitors, often fleshy seaweeds, and may also result in explosions of predator populations. (*v*) Combinations of stress appear to be associated with threshold responses and ecological surprises, including devastating pathogen outbreaks. (*vi*) The fossil record suggests that corals as a group are more likely to suffer extinctions than some of the groups that associate with them, whose habitat requirements may be less stringent.

Coral reefs are often called the rainforests of the sea, although calling rainforests the coral reefs of the land might be even more appropriate (1). As with rainforests, the importance of coral reefs lies not so much in the diversity of the corals themselves, but rather in the millions of species that live primarily or exclusively in association with them. Veron (2), for example, gives a minimum estimate of 835 species of reef-building corals, and estimates for the biodiversity of reefs overall range from 1–9 million (3).

Unfortunately, modern human civilization and coral reefs make poor companions. Most activities of people (e.g., fishing, deforestation, nutrient enrichment, burning of fossil fuels, and use of toxic chemicals) either damage corals directly or damage them indirectly by adversely modifying interactions with their competitors, predators, pathogens, and mutualists. For example, Edinger and colleagues (4) document losses in coral species diversity ranging from 30–60% on reefs degraded by human activities, with a 25% loss in generic diversity on two of these reefs over just 15 years. Thus, although concerted efforts to protect reef habitats may slow their ongoing decline, it is difficult to be optimistic about the health of reefs globally over the short term in the context of increasing human populations and economic growth (5).

As the world changes with growing human domination, ecological and evolutionary changes on coral reefs similar to those outlined for terrestrial and other marine organisms and ecosystems (e.g., refs. 116–118 and other articles in this colloquium) are inevitable. A few factors do work in the favor of coral reefs. For example, the widely dispersing larvae and still large population sizes of many important reef builders probably provide some protection against extinction (6). The diversity of coral reef ecosystems may also make catastrophic invasions of exotic species less likely, although invasibility may increase with disturbance (7) and the degree to which diversity *per se* inhibits invasions remains unclear (8). The fossil record clearly shows, however, that marine species and ecosystems have their limits (refs. 119 and 120 and other articles in this colloquium), and the recent record indicates that these limits may be approached with little warning (9, 10). The broader ecological consequences of reducing biodiversity (11) remain essentially uninvestigated for coral reefs. Indeed, our understanding of even the basic physical parameters of global change of relevance to reefs is inadequate (12).

Below I focus on some of the peculiar features of corals and other reef dwellers that are likely to affect their ecological and evolutionary futures. Many of the examples are drawn from the Caribbean, because change (and thus a possible glimpse of the future) has been much greater there over the last several decades. Nevertheless, the major points have applicability to reefs worldwide.

Reproduction: Allee Effects, Inbreeding, and Hybridization

Sessile marine organisms, with very few exceptions, depend on water to bring their gametes together; either eggs and sperm are both released into the water column or eggs are fertilized internally by sperm picked up from the water column. One immediate consequence is that low gamete densities caused by low population densities, asynchronous reproduction, or low reproductive output per individual can lead to reproductive failure (13, 14), a classic example of an Allee effect (15).

Corals themselves are commonly hermaphroditic and exhibit two primary types of reproductive strategies: broadcasting and brooding (16, 17). Physically large and long-lived coral species, the primary reef builders, are typically broadcasters that reproduce once or twice a year during an event known as mass spawning. Buoyant bundles of eggs glued together with sperm are released in approximate synchrony on just a few nights of the year, when they float to the surface, break apart, and with luck achieve fertilization. The small larvae of broadcasting species typically disperse for at least 4 days (17).

As with other outbred marine invertebrates (18), species in this group do not generally self-fertilize successfully (17). Thus, eggs from one colony need to reach sperm from another for reproduction to succeed. For broadcasting corals, we know very little about critical gamete densities necessary for supporting successful fertilization. The best study is that of Oliver and Babcock (19), who showed that fertilization rates drop to low levels by 3 h after peak spawning and on nights other than the major night of spawning. This suggests that colonies spawning in

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temporal or spatial isolation (measured on the scale of a few hours and tens or at most hundreds of meters) will often experience nearly complete reproductive failure. Adverse environmental conditions can also reduce fertilization rates independent of gamete density (20, 21). Moreover, nearby colonies may release few gametes and thus be ineffective mating partners if they are recovering from stressful conditions or damage (21–24) or are small for whatever reason [size rather than age determines reproductive output (25, 26), so that fragments typically have reduced fecundity or are infertile (22, 27)]. Thus, reef degradation may lead to sharply reduced reproduction, not only because of lowered gamete production, but also because of reduced rates of fertilization for those gametes that are released.

However, eggs failing to encounter conspecific sperm will not necessarily remain unfertilized, even when self-fertilization is not feasible, because simultaneous or nearly simultaneous spawning provides potential opportunities for interspecific hybridization (2). The extent to which this happens is a matter of debate, because some species are clearly separated by either subtle temporal differences in spawning time or gametic incompatibilities (28). However, these barriers are likely to become less effective as opportunities for conspecific matings decrease. For example, mechanisms to prevent selfing often decline in efficacy after 4 h (29), and the same might happen with gametic barriers to interspecific fertilization. Similarly, subtle temporal differences in spawning times between species whose gametes are otherwise compatible (28) would be less effective if, for example, unfertilized eggs from an early spawning species remained near populations of later spawning species. Laboratory experiments do clearly suggest that many species are capable of hybridization, including species with very different morphologies (30, 31). However, the potential evolutionary impact of hybridization between morphologically and ecologically distinct taxa is difficult to evaluate empirically, because of long generation times and the difficulty of maintaining corals in captivity for determining long-term survival and fertility of hybrids.

Brooding corals exhibit a very different reproductive strategy. Only sperm are released, and fertilized eggs are retained within the colony and released as swimming planula larvae. These corals often reproduce on a lunar cycle for a number of months per year (25), and the large larvae that are released probably do not travel far, despite their physiological potential to do so without feeding, thanks to the zooxanthellae that brooded larvae contain (32). For example, Carlon and Olson (33) found that the average swimming time for the larvae of the brooding coral *Favia fragum* was only about 4 min. Such limited dispersal suggests that biparental inbreeding (mating between relatives) is not uncommon in brooding corals (17). Distances between potential mates are probably even shorter than they are for broadcasting species, perhaps as little as a few meters (34). However, brooding species are more likely to be able to self-fertilize (17, 35), probably as a consequence of regular biparental inbreeding (18). Thus, one likely consequence of habitat deterioration and destruction is an increase in selfing as distances between fertile colonies increase.

Compared with the mass spawning species, brooding corals have many of the attributes of weeds: they often grow to smaller sizes, reproduce earlier, have shorter life spans, and are competitively inferior to larger and more aggressive broadcasting species (25, 26, 36). Moreover, their ability to self-fertilize would make them less vulnerable to Allee effects and allow them to persist even at low densities. Brooding corals have come to dominate many Caribbean reefs following disturbances of the 1980s and 1990s (37), and they also succeeded disproportionately during the Oligocene–Miocene extinction event (38). Nevertheless, brooding corals are very vulnerable to some forms of disturbance, including high-temperature disruption of their symbiotic associations (39), to which I now turn.

Coral–Algal Symbiosis

One of the striking features of coral reefs is the intimate nutritional symbiosis between the coral animal and single celled dinoflagellates, typically known as zooxanthellae. Corals provide excretion products to their algal guests, which in turn provide photosynthetic products to their coral hosts (40). All reef-building corals are obligately dependent on their zooxanthellae, which are probably responsible for the characteristically high rates of calcification that reef-building corals achieve (41).

The ecological balance between corals and their algal partners, and hence the success of corals as reef builders, is potentially very sensitive to environmental conditions. This stems from the fact that although we tend to think of mutualisms as cooperative relationships, they are often better viewed as reciprocally selfish associations (42). That is, other things being equal, each partner tries to maximize its net gain from the association by minimizing costs and maximizing benefits. This selfishness has the potential to lead to ecological instability, because if stress makes it difficult for one partner to provide its normal complement of benefits, the other partner may respond in the short term by terminating the relationship, a strategy that is normally an appropriate response to the ever present threat of cheaters [partners that receive but do not return benefits (42)].

The implications of this are more than academic in the context of the environmental changes to which reefs are subject today. When corals are exposed to elevated temperatures or UV radiation, for example, they "bleach"—that is, photosynthetic pigments are drastically reduced, typically because of algal death or expulsion (43). Bleached corals can survive without their normal complement of zooxanthellae for weeks or sometimes months, but their growth and reproductive output are reduced and eventually they die. Global warming is of particular concern, because temperatures as little as 1°C over the normal seasonal maximum can provoke substantial bleaching (44). Coral bleaching has increased dramatically over the last several decades (44), and 1998 (with its unusually strong El Niño) was characterized by massive bleaching on a worldwide scale (45). In some areas, reefs were decimated to unprecedented extents, based on the fossil record (39), and climate models suggest that temperatures sufficient to induce bleaching could become annual events within a few decades (45).

Nevertheless, it remains unclear whether coral reefs as we know them will succumb to global warming, because coral–algal symbioses do have some capacity to increase their ability to withstand stresses such as high temperatures. For many years, physiological acclimatization was viewed as the primary mechanism (46), and recent studies have shown, for example, that acclimation to high light can provide some protection against high temperature (47). There is also renewed interest in evolutionary responses with the realization that zooxanthellae have far more genetic diversity than previously realized. Pioneering studies by Trench (48) and Rowan (49) have shown that what was once viewed as a single species living in association with multiple invertebrate phyla, is in fact a diverse assemblage, now shown to consist of at least four major clades (50, 51) whose genetic differences are comparable to those exhibited between different families or orders of free-living dinoflagellates (49). Some coral species host just one type of symbiont, whereas other corals host multiple types, sometimes within individual colonies (49–51).

This diversity is of particular significance with respect to global change, because different types of zooxanthellae exhibit striking differences in their susceptibility to bleaching (52) and their ability to recolonize bleached hosts (53). Thus, reefs may be able to survive predicted increases in sea temperature and other coming environmental changes by shifts in the kinds of zooxanthellae that are typically hosted by corals. Indeed, even bleaching itself may be adaptive if it facilitates symbiont exchange (54).

Experimental bleaching does appear to result in novel associations (51, 53) but we know almost nothing about the long-term consequences of such shifts in symbiont associations. Symbionts that initially colonize bleached colonies are probably rapidly growing opportunistic genotypes (53) that may not be ideal partners from the coral's perspective. These may subsequently be replaced by stress-resistant mutualists (53), but again we do not know how these associations perform as mutualisms relative to those that were established before bleaching. Thus, although opportunistic or stress-resistant symbionts may provide protection against outright mortality (51), the consequences for growth rates or reproductive output are unclear.

Global warming is not the only aspect of global change with which corals and their symbionts must contend. Many aspects of the oceans' biogeochemistry are changing in response to human activities (55). Rising levels of carbon dioxide that underlie much of global warming may be detrimental in their own right to corals. Coral reef growth depends on the net accumulation of calcium carbonate, which is affected by the saturation state of calcium carbonate in surface waters. Kleypas and colleagues (56) argue that by 2100, increased levels of carbon dioxide might cause calcification to decrease by 17–35% relative to preindustrial levels. Such a decrease could result in weaker coral skeletons, reduced growth rates, increased susceptibility to erosion, and perhaps even a reduction in the ability of higher latitudes (a potential refuge from higher temperatures) to sustain reef growth (57).

Increased nutrients of the types associated with changing land-use patterns (58) may also directly harm corals. High nutrient levels can result in reduced rates of growth and calcification (59), as well as decreases in reproduction (60), probably because of their impact on the symbiotic association between corals and zooxanthellae (40, 59). Nevertheless, experimental manipulations of nutrient levels on corals often yield slight and sometimes unexpected results, particularly when done in the field (61). Thus, it remains unclear whether current levels of eutrophication are having a major, direct effect on the health of corals. However, nutrients may also have a variety of indirect effects that are discussed in later sections.

Emergent Diseases

Dinoflagellates are not the only important microbes on reefs. Although poorly known, pathogens probably greatly outnumber mutualists, and they are capable of completely transforming reef communities through their effects on ecologically dominant organisms. The most spectacular example of disease in the oceans is the decimation of the once abundant sea urchin *Diadema antillarum* throughout the tropical western Atlantic. Between 1983 and 1984, more than 95% of these urchins died because of a still uncharacterized pathogen that swept through the entirety of the urchin's geographic range with the exception of the eastern Atlantic (62). Nearly two decades later, recovery is still limited (63), and in many places densities remain extremely low, despite the relatively short generation times and high fecundity of *Diadema* (64). Although reasons for the failure of *Diadema* to recover may be complex, the effect of low density on fertilization rates is probably a major contributor (64).

Reef-building corals themselves appear to be increasingly affected by disease (65). The ecological effects of coral pathogens are likely to be especially severe because rates of mortality can be very high [up to 2 cm of coral tissue daily (66)], whereas coral growth and recruitment rates are typically intrinsically low [e.g., annual growth rates of ≈1 cm per year in many massive corals (67)]. The Caribbean, once again, provides particularly troubling examples (68). Before 1980, shallow-water reefs throughout the region were dominated by the genus *Acropora*. By 1990, most stands of *Acropora* were reduced to scattered small patches by an unknown pathogen. Recovery has been slight (65), despite the relatively high growth rates that characterize the genus. Recovery from diseases of massive corals is likely to be especially prolonged because growth rates in these corals are far slower (67). Diseases that attack *Montastraea* (69) are perhaps the most threatening to Caribbean reefs, because of the dominance of this coral as a reef builder throughout the region.

The direct evolutionary impact of disease on coral reefs remains unclear. Lessios (62) found no evidence for reduced genetic variation in *Diadema* following catastrophic mortality, perhaps because even 95% mortality does not result in small enough populations sizes in formerly abundant organisms. Alternatively, the bottleneck in population size may not have persisted long enough at the time of the study for genetic effects to accumulate. The ecological impacts of diseases on reefs are already substantial, however, via the direct effects of coral pathogens on coral abundance and the indirect effects of the demise of a dominant herbivore on seaweeds (discussed below). These ecological changes appear to be without precedent over at least the last several thousand years, based on examination of the extensive Caribbean fossil reef record (70–72).

As with any recent change, evaluating the role of anthropogenic effects is a challenge. This is particularly true for marine diseases, because there is almost no baseline information on earlier disease prevalence and even the pathogens responsible are largely unknown (65, 68). Harvell and colleagues (68) suggest that apparent increases in the incidence of disease in marine ecosystems generally could be at least in part the consequence of global climate change, and they note that terrestrial activities of man appear to have introduced at least one pathogenic agent to coral reefs via run-off. It has long been recognized that stress can make corals vulnerable even to normally benign microbial associates (73), and thus, disease seems likely to be a major player on reefs of the future. The ability of corals to respond evolutionarily to the threat of pathogens is probably fairly limited, given the enormous difference in generation times between corals and their microbial enemies.

Shifting Ecological Balances: Competitors and Predators of Corals

Pathogens are not the only biological enemies of corals; substantial mortality is also associated with overgrowth by competitors and the feeding of predators. Evidence for increases in these sources of mortality in recent decades is accumulating, thereby suggesting that corals are currently waging a losing battle on this front as well.

The most important competitors of corals today on most reefs are seaweeds (74). There is general agreement that the competitive balance between corals and macroalgae is shaped primarily by the magnitude of herbivory and nutrient availability, but their relative importance and how they interact continues to be the subject of debate (75–77). Small-scale experiments suggest, however, that herbivory is often likely to be much more important than nutrients in limiting algal growth (78).

The histories of Kaneohe Bay, Hawaii (79) and Discovery Bay, Jamaica (37) illustrate many of the relevant issues on a broader scale. Concerns about eutrophication related to the explosion of the green bubble alga *Dictyosphaeria cavernosa* led to the diversion of sewage from Kaneohe Bay beginning in 1977, and the opportunity to monitor the response of the reef community to this major, albeit uncontrolled, experiment (79). By 1983, algal abundance had dropped to 25% of peak levels and coral abundance had increased. Since then, however, algal cover has again increased and coral recovery has slowed or even been reversed. In the case of Discovery Bay (37), the uncontrolled experiment was the Caribbean-wide die-off of the herbivorous sea urchin *D. antillarum* described above, which at any one site occurred over the course of only a few days (62). In Discovery Bay (which was in the process of recovering from a major hurricane several years earlier) dead substrates were quickly colonized by small ephemeral algae, but these were replaced over several years by larger, long-lived species capable of overgrowing living coral. The result has been the decline of coral cover from 52% to 3%, and the increase in algal cover from 4% to 92% (37). Similar changes, albeit somewhat different in timing and extent, have occurred elsewhere (62). The general consensus is that the die-off of such an important herbivore, particularly in the context of low abundance of herbivorous fishes due to overfishing, was the primary cause of the shift from a coral-dominated to an algal-dominated reef (37, 75, 77).

These events suggest that herbivory is often the more important regulator of competition between algae and corals, although eutrophication can also shift the balance toward algal overgrowth, particularly when it is extreme (as in Kaneohe Bay). Algae are not the only competitors of corals that could be affected by eutrophication, however; nutrient enrichment and consequent increases in bacterial populations might also facilitate the success of filter-feeders that have few natural predators and are capable of overgrowing corals. The ascidian *Trididemnum solidum*, which increased on reefs of Curaçao by 900% between 1978 and 1993 (80), may be a case in point, although no data showing the cause of the increase exist. In any case, because the effects of both decreased herbivory and increased eutrophication are likely to be augmented in the future, the future of corals will almost certainly include increases in mortality from competitors.

The same anthropogenic factors that can affect the competitors of corals—eutrophication and overfishing—have also been implicated in some of the spectacular explosions in predators of corals (corallivores) witnessed over the last few decades. The crown-of-thorns starfish, *Acanthaster planci*, is the most infamous of these (81, 82), but explosions of predatory snails, particularly in the genus *Drupella*, have also been noted (83). At least in the case of *Acanthaster*, the extent of outbreaks appears to be unprecedented, because the size structure of corals preceding the earliest documented outbreaks could not have existed if current magnitudes and frequencies of outbreaks were a long-term feature of reefs (84). Outbreaks also appear to be shifting in nature from episodic to chronic (82). As with the competitors of corals, fishing out of predators on corallivores (top-down control) may play a larger role than the enhancement of survivorship of corallivores in the larval stage by eutrophication (bottom-up control; ref. 82). However, not all studies support the importance of the former (85) or the lack of importance of the latter (86). The factors contributing to *Drupella* outbreaks are even less well understood (83).

Sea Level, Storms, and Bioerosion

One of the most frequently discussed consequences of global climate change is rising sea level. Past rises in sea level have often been associated with global increases in reef development (87), but rapid sea level rise can also result in the drowning of reefs if it is too rapid, because of the light dependency of coral–algal symbiosis and declining light levels with increasing depth. Reef drowning is of potential concern because projected rates of future sea level rise come close to estimates of past sustained rates of reef accretion before the onset of anthropogenic effects (12). Although recruitment of newly submerged areas could keep many species from going extinct, the three-dimensional complexity of a true reef, on which other organisms depend, would be lost.

Net vertical reef accretion is a balance between growth and destruction (88), so that any of the features discussed previously that slow coral growth have the potential to contribute to reef drowning. However future global change is also likely to affect processes on the other side of the equation—in particular, reef destruction via storms and the activities of organisms that bore into or scrape the surfaces of calcium carbonate skeletons (bioeroders). Both bioerosion and storminess have been projected to increase in response to anthropogenic global change, the former because of the association between eutrophication and the nutrition of bioeroders (88), and the latter because of the association between high temperatures and cyclonic storms (12). The likely extent of these changes remains subject to debate, but either could result in a slowdown of reef accretion (88). Such a slowdown increases the probability that reefs will not be able to keep up with rising sea levels.

Increased bioerosion and storminess will probably have specific evolutionary consequences in addition to their general effects on reef growth. Fragmentation can facilitate production and spread of asexual propagules, but it is often costly for the organisms involved because many fragments die and survivors have lowered fecundity (22, 27). Thus, increased bioerosion and storminess should favor strong skeletons or the ability to propagate effectively by fragmentation. On the other hand, rising sea level should lead to selection for rapid vertical growth. Some of these selective effects may operate within species, but most will probably favor some species at the expense of others. However, because coral species with very dense skeletons are often slowly growing, and fragmentation results in lowered three-dimensionality, reefs of the future may find themselves caught evolutionarily between the proverbial rock and a hard place.

Threshold Effects, Multiple Stable States, and Metapopulations

Reef biologists who have watched coral cover decline from 50% to 5% over the course of their careers are understandably distressed by the state of reefs today and their prospects for the future. But even more alarming than the magnitude of the decline has been its speed and the fact that few scientists saw it coming. For example, by 1980 the reefs of Discovery Bay, Jamaica had been studied for decades and overfished for centuries (89). Nevertheless, the implications of extreme overfishing for resiliency of these reefs to subsequent disturbances was not appreciated until recovery failed.

Several common attributes of biological systems make prediction difficult. The first are threshold effects or breakpoints (90). These quintessentially nonlinear relationships are common, but nevertheless often surprising: when the thermostat is turned up one notch, people tend to expect one notch's worth of additional heat, not a house in flames. Responses to single variables can behave in this fashion; for example, calcification may remain constant over a range of saturation states, but then drop abruptly below some threshold value (56). Allee effects are classic threshold phenomena, because populations increase above a minimum population size but decrease below it (15).

When two variables interact synergistically, threshold responses and ecological surprises are probably even more likely (91, 92). For example, neither sedimentation nor high nutrient levels are good for corals, but their combined effect is far worse, because fine muds then aggregate into a smothering marine "snow" (93). Similarly, the collapse of reef ecosystems along the north coast of Jamaica seems to have resulted from the synergistic interaction of overfishing and disease (37). Unfortunately, our understanding of how multiple stressors interact remains limited (94, 95).

Also coupled with threshold dynamics is the concept of multiple stable states (9, 90). The existence of multiple stable states implies that two different ecological communities can be stable under the same conditions, with history determining which community is present at any particular point in time. Multiple stable points are linked with threshold effects because it is often the case that the position of the breakpoint depends on the direction in which the community is moving. For example, a switch from coral dominance to algal dominance might occur at specific levels of eutrophication and herbivory, but much lower nutrient levels or higher levels of herbivory might be required to shift the system back to its original coral-dominated state. This pattern of response is well known for lakes (96), and there is no reason in principle that it might not apply to coral reefs (9).

Switches from coral dominance to algal dominance are dramatic, but they are not the only cause for concern. As on land, potential coral reef habitat is being eliminated and fragmented with the spread of destructive processes both in the sea and on the shore. Models considering this aspect of changing spatial structure provide disturbing insights. For example, in a simple two-species model, habitat destruction (removal of suitable patches) can result in the extinction of a competitive dominant that disperses poorly at the expense of a competitively inferior species that disperses well, even when remaining patches undergo no intrinsic changes themselves (97). More elaborate versions of this idea predict a certain percentage of inevitable extinctions over time associated with a certain fraction of habitat loss—a so-called "extinction debt"—again affecting competitively dominant species first and rising sharply as habitat loss increases (98). Estimates of 40% reef habitat loss through irreparable damage over the next several decades (5) are sobering in this context, because the models imply that competitively dominant corals, which are often major reef builders, may not be able to persist even in areas not strongly impacted by the activities of people.

Applications of these models to specific coral reef situations are limited and require careful consideration of how model concepts and terms relate to the biology of reef organisms. Stone (99, 100) analyzed a Red Sea reef flat and concluded that numbers of species extinctions associated with habitat reduction would be especially catastrophic because competitively dominant corals were already rare. However, this result reflects the fact that reef flats are regularly disturbed and, thus, always dominated by weedy corals. In contrast, the major reef builders on Caribbean reefs are (or were until recently) competitively dominant species, either via aggressive interactions or their ability to overtop their neighbors, whereas weedy corals are typically small understory forms. Here, the number of species extinctions might be smaller, but the ecological impact larger. Records of sea level changes in the fossil record are particularly interesting in this context. Pandolfi (101) has shown that habitat loss of 90% associated with a marked drop in sea level about 18,000 years ago resulted in the rapid extinction of two coral species (which were, as predicted by the models, competitive dominants).

The models (97, 98), as they have been applied to reefs to date (99, 100), assume that each patch is occupied by a single species. In this sense, the analyses describe the dynamics on single reefs, with patches being de facto the spaces occupied by individual colonies. Metapopulation models in the strict sense describe patches surrounded by uninhabitable area, with rates of colonization between populations being slower than the dynamics within populations (ref. 102, and papers in this colloquium). This structure is more appropriate for describing regional dynamics—for example, the many reefs of Caribbean islands and banks separated by uninhabitable deep water that is only occasionally crossed by propagules (103). Marine organisms with limited dispersal abilities that occasionally disperse long distances by rafting (104) almost certainly meet these assumptions, but even organisms once assumed to be too widely dispersing to conform to metapopulation models have recently been shown to recruit to parental populations to a surprising extent (105–107). We do not currently have nearly enough information to parameterize a regional metapopulation model for coral reefs in a quantitatively useful way (103). It is worth noting, however, that at this spatial scale the true weeds might not be corals at all, because broadcasting corals can potentially travel but rarely successfully recruit, whereas brooders regularly recruit, but not at long distances. The weeds would instead be the rapidly colonizing ephemeral algae seen on reefs after hurricanes and other major disturbances.

Broader Consequences for Biodiversity

The extent to which degraded reefs and other habitats can support the associated diversity of healthy coral reef habitats—the current homes for the myriad crustaceans, worms, mollusks, bryozoans, and other groups that are found on reefs—is unknown. Given that reef associates have many times the diversity of the corals themselves, several issues are relevant: (*i*) Are reefs as ecosystems especially vulnerable to environmental change or slow to recover? (*ii*) Are reef dwellers less vulnerable than corals themselves? The fossil record of past extinctions provides the only real data for evaluating these questions.

It is often stated that reef ecosystems are both more vulnerable to extinction and slower to recover, but rigorous analyses are surprisingly limited (87). Past extinction events appear to have had a diverse suite of causes, not surprisingly, because global change in any direction from the status quo is likely to accelerate extinction; this probably explains why there is no strong bias against tropical ecosystems overall. Within the tropics, however, it does appear that shallow-water, low-nutrient carbonate platforms have been more vulnerable than other tropical environments, although there is no strong evidence that such ecosystems recover more slowly (87). There is also a limited amount of evidence suggesting that photosymbiotic organisms might have been more vulnerable to extinction than nonphotosymbiotic organisms, both at the end of the Cretaceous (87) and during the more minor Oligocene–Miocene extinction (108). Corals were also more vulnerable to the changes associated with the rise of the Isthmus of Panama; there are no living examples of closely related sister species among the zooxanthellate scleractinian corals on the two sides of the Isthmus, whereas such sister taxa are common in other groups (109).

One possible explanation for this pattern relates to differences in distributions between the groups. Many organisms characteristic of coral reefs are not restricted to reefs (87). This is true of corals themselves, of course, which can be found growing as scattered colonies without creating the three-dimensional structure and complexity that the term reef implies. However, extrareef distributions are likely to be even more characteristic of other groups of reef-dwellers, at a variety of taxonomic levels. In fishes, for example, all families considered typical of reefs have ranges that extend outside the boundaries of reefs (110, 111). Similarly in bryozoans, more than 75% of reef-associated species of the Caribbean are also found in nonreefal settings (112). Should this be a general pattern, which seems likely, then even elimination of most coral reef habitats would probably not result in the extinction of a comparable proportion of coral reef builders and dwellers (87). No taxonomically comprehensive analysis of obligate versus facultative reef associates exists, but the above suggests that even the loss of all true reefs would leave many facultative reef associates as survivors, and thus many of the deeper branches of the tree of life intact (113).

The most relevant guides to the future are, of course, past extinctions associated with changes similar to those projected for the coming century. Unfortunately, we have little to guide us in this regard. Mass extinctions have been intensively studied, but they are remote in time and, hence, involve organisms whose phylogenetic affinities are distant from the organisms whose responses we wish to predict. Moreover, despite the alarming nature of the ongoing anthropogenic extinctions, they do not begin to approach the severity of these cataclysmic events (ref. 119 and other articles in this colloquium); if they do, *Homo sapiens* will have a lot more to worry about than the future of coral reefs. The most relevant comparisons are with the Oligocene–Miocene and Pliocene–Pleistocene extinctions (38, 108, 114), but both of these events involved cooling episodes rather than global warming. The combination of nutrification, global warming, and loss of top members of the food chain (not to speak of novel, introduced chemicals) is unprecedented over the last 65 million years. Thus, it is perhaps not surprising that many of the reef organisms that persisted and thrived during the most recent biological upheavals are those that are suffering the most now (114). Who the winners will be this time around is impossible to predict, but we may not be that happy with the outcome.

The Camel's Last Straw?

In the face of so many unknowns, qualitative analogies can provide an important complement to quantitative analyses. For this reason I close with the concept of the straw that broke the camel's back. No single straw "causes" ecological collapse; collapse is difficult to predict based on the response of the camel to earlier straws, but once collapse occurs, the camel does not return to its feet when the last straw is removed. The recent history of coral reefs suggests that collapse is not impossible, and indeed, that we may be closer to worldwide collapse than we realize. Moreover, the weight of the straws is likely to be multiplicative rather than additive because of negative synergistic effects between different types of stressors. Crippled coral reefs, like crippled camels, provide many fewer services, and they can be prohibitively expensive to repair (115). Although reefs are more likely than camels to recover unaided, having come and gone and come again throughout the history of life, it is likely to be a very slow process, and we may not be around to see true reefs when they do return.

1. Davidson, O. G. (1998) *The Enchanted Braid* (Wiley, New York).
2. Veron, J. E. N. (1995) *Corals in Space and Time: The Biogeography and Evolution of the Scleractinia* (Univ. of New South Wales Press, Sydney).
3. Reaka-Kudla, M. L. (1997) in *Biodiversity II: Understanding and Protecting Our Biological Resources*, eds. Reaka-Kudla, M. L., Wilson, D. E. & Wilson, E. O. (Joseph Henry Press, Washington, DC), pp. 83–108.
4. Edinger, E. N., Jompa, J., Limmon, G. V., Widjatmoko, W. & Risk, M. J. (1998) *Mar. Pollut. Bull.* **36,** 617–630.
5. Wilkinson, C. R. (1999) *Mar. Freshwater Res.* **50,** 867–878.
6. McKinney, M. L. (1998) *Diversity Distrib.* **4,** 3–8.
7. Vermeij, G. J. (1991) *Science* **253**, 1099–1104.
8. Levine, J. M. & D'Antonio, C. M. (1999) *Oikos* **87**, 15–26.
9. Knowlton, N. (1992) *Am. Zool.* **32,** 674–682.
10. Done, T. J. (1992) *Hydrobiologia* **247**, 121–132.
11. Chapin, F. S., III, Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., *et al.* (2000) *Nature (London)* **405,** 234–242.
12. Pittock, A. B. (1999) *Am. Zool.* **39**, 10–29.
13. Levitan, D. R. & Petersen, C. (1995) *Trends Ecol. Evol.* **10**, 228–231.
14. Levitan, D. R. (1998) in *Sperm Competition and Sexual Selection*, eds. Birkhead, T. R. & Moller, A. P. (Academic, San Diego), pp. 175–217.
15. Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999) *Trends Ecol. Evol.* **14,** 405–410.
16. Richmond, R. H. & Hunter, C. L. (1990) *Mar. Ecol. Prog. Ser.* **60,** 185–203.
17. Carlon, D. B. (1999) *Trends Ecol. Evol.* **14,** 491–495.
18. Knowlton, N. & Jackson, J. B. C. (1993) in *The Natural History of Inbreeding and Outbreeding*, ed. Thornhill, N. W. (Univ. Chicago Press, Chicago), pp. 200–249.
19. Oliver. J. & Babcock, R. (1992) *Biol. Bull. (Woods Hole, Mass.)* **183,** 409–417.
20. Gilmour, J. (1999) *Mar. Biol. (Berlin)* **135,** 451–462.
21. Omori, M., Fukami, H. & Hatta, M. (2001) *Limnol. Oceanogr.*, in press.
22. Lirman, D. (2000) *J. Exp. Mar. Biol. Ecol.* **251,** 41–57.
23. Guzmán, H. M. & Holst, I. (1993) *Mar. Pollut. Bull.* **26,** 276–282.
24. van Veghel, M. L. J. & Bak, R. P. M. (1994) *Mar. Ecol. Prog. Ser.* **109,**229–233.
25. Soong, K. (1993) *Coral Reefs* **12,** 77–83.
26. Soong, K. & Lang, J. C. (1992) *Biol. Bull. (Woods Hole, Mass.)* **183,** 418–431.
27. Smith, L. D. & Hughes, T. P. (1999) *J. Exp. Mar. Biol. Ecol.* **235,** 147–164.
28. Knowlton, N., Maté, J. L., Guzmán, H. M., Rowan, R. & Jara, J. (1997) *Mar. Biol. (Berlin)* **127,** 705–711.
29. Heyward, A. J. & Babcock, R. C. (1986) *Mar. Biol. (Berlin)* **90,** 191–195.
30. Willis, B. L., Babcock, R. C., Harrison, P. L. & Wallace, C. C. (1997) *Coral Reefs* **16,** Suppl., S53–S65.
31. Hatta, M., Fukami, H., Wang, W., Omori, M., Shimoike, K., Hayashibara, T., Ina, Y. & Sugiyama, T. (1999) *Mol. Biol. Evol.* **16,** 1607–1613.
32. Richmond, R. H. (1987) *Mar. Biol. (Berlin)* **93,** 527–533.
33. Carlon, D. B. & Olson, R. R. (1993) *J. Exp. Mar. Biol. Ecol.* **173,** 247–263.
34. Morse, A. N. C., Iwao, K., Baba, M., Shimoike, K., Hayashibara, T. & Omori, M. (1996) *Biol. Bull. (Woods Hole, Mass.)* **191,** 149–154.
35. Brazeau, D. A., Gleason, D. F. & Morgan, M. E. (1998) *J. Exp. Mar. Biol. Ecol.* **231,** 225–238.
36. Loya, Y. (1976) *Nature (London)* **259,** 478–480.
37. Hughes, T. P. (1994) *Science* **265,** 1547–1551.
38. Edinger, E. N. & Risk, M. J. (1995) *Paleobiology* **21,** 200–219.
39. Aronson, R. B., Precht, W. F., Macintyre, I. G. & Murdoch, T. J. T. (2000) *Nature (London)* **405,** 36.
40. Falkowski, P. G., Dubinsky, Z., Muscatine, L. & McCloskey, L. (1993) *Bioscience* **43,** 606–611.
41. Gattuso, J.-P., Allemand, D. & Frankignoulle, M. (1999) *Am. Zool.* **39,** 160–183.
42. Herre, E. A., Knowlton, N., Mueller, U. G. & Rehner, S. A. (1999) *Trends Ecol. Evol.* **14,** 49–53.
43. Brown, B. E. (1997) *Coral Reefs* **16,** Suppl., S129–S138.
44. Glynn, P. W. (1993) *Coral Reefs* **12,** 1–17.
45. Hoegh-Guldberg, O. (1999) *Mar. Freshwater Res.* **50,** 839–866.
46. Gates, R. D. & Edmunds, P. J. (1999) *Am. Zool.* **39,** 30–43.
47. Brown, B. E., Dunne, R. P., Goodson, M. S. & Douglas, A. E. (2000) *Nature (London)* **404,** 142–143.
48. Trench, R. K. (1997) *Proc. 8th Int. Coral Reef Symp.* **2,** 1275–1286.
49. Rowan, R. (1998) *J. Phycol.* **34,** 407–417.
50. Toller, W. W., Rowan, R. & Knowlton, N. (2001) *Biol. Bull. (Woods Hole, Mass.)*, in press.
51. Baker, A. C. (1999) Dissertation (Univ. of Miami, Coral Gables, FL).
52. Rowan, R., Knowlton, N., Baker, A. & Jara, J. (1997) *Nature (London)* **388,** 265–269.
53. Toller, W. W., Rowan, R. & Knowlton, N. (2001) *Biol. Bull. (Woods Hole, Mass.)*, in press.
54. Buddemeier, R. W. & Fautin, D. G. (1993) *Bioscience* **43,** 320–326.
55. Falkowski, P. G., Barber, R. T. & Smetacek, V. (1998) *Science* **281,** 200–206.
56. Kleypas, J. A., Buddemeier, R. W., Archer, A., Gattuso, J.-P., Langdon, C. & Opdyke, B. N. (1999) *Science* **284,** 118–120.
57. Kleypas, J. A., McManus, J. W. & Meñez, L. A. B. (1999) *Am. Zool.* **39,** 146–159.
58. Downing, J. A., McClain, M., Twilley, R., Melack, J. M., Elser, J., Rabalais, N. N., Lewis, W. M., Jr., Turner, R. E., Corredor, J., Soto, D., *et al.* (1999) *Biogeochemistry* **46,** 109–148.
59. McGuire, M. P. & Szmant, A. M. (1997) *Proc. 8th Int. Coral Reef Symp* **1,** 909–914.
60. Ward, S. & Harrison, P. (2000) *J. Exp. Mar. Biol. Ecol.* **246,** 179–221.
61. Hoegh-Guldberg, O., Takabayashi, M. & Moreno, G. (1997) *Proc. 8th Int. Coral Reef Symp.* **1,** 861–866.
62. Lessios, H. A. (1988) *Annu. Rev. Ecol. Syst.* **19,** 371–393.
63. Edmunds, P. J. & Carpenter, R. C. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5067–5071. (First Published March 27, 2001; 10.1073/pnas.071524598)
64. Lessios, H. A. (1995) *Proc. R. Soc. London Ser. B* **259,** 331–337.
65. Richardson, L. L. (1998) *Trends Ecol. Evol.* **13,** 438–443.
66. Richardson, L. L., Goldberg, W. M., Kuta, K. G., Aronson, R. B., Smith, G. W., Ritchie, K. B., Halas, J. C., Feingold, J. S. & Miller, S. L. (1998) *Nature (London)* **392,** 557–558.
67. Jackson, J. B. C. (1991) *Bioscience* **41,** 475–482.
68. Harvell, C. D., Kim, K., Burkholder, J. M., Colwell, R. R., Epstein, P. R., Grimes, D. J., Hofmann, E. E., Lipp, E. K., Osterhaus, A. D., Overstreet, R. M., *et al.* (1999) *Science* **285,** 1505–1510.
69. Santavy, D. L., Peters, E. C., Quirolo, C., Porter, J. W. & Bianchi, C. N. (1999) *Coral Reefs* **18,** 97.
70. Pandolfi, J. M. & Jackson, J. B. C. (1997) *Proc. 8th Int. Coral Reef Sym.* **1,** 397–404.
71. Aronson, R. B., Precht, W. F. & Macintyre, I. G. (1998) *Coral Reefs* **17,** 223–230.
72. Greenstein, B. J., Curran, H. A. & Pandolfi, J. M. (1998) *Coral Reefs* **17,** 249–261.
73. Mitchell, R. & Chet, I. (1975) *Microb. Ecol.* **2,** 227–233.
74. Miller, M. W. (1998) *Oceanogr. Mar. Biol. Annu. Rev.* **36,** 65–96.
75. Hughes, T. P., Szmant, A. M., Steneck, R., Carpenter, R. & Miller, S. (1999) *Limnol. Oceanogr.* **44,** 1583–1586.
76. Lapointe, B. E. (1999) *Limnol. Oceanogr.* **44,** 1586–1592.
77. McCook, L. J. (1999) *Coral Reefs* **18,** 357–367.
78. Miller, M. W., Hay, M. E., Miller, S. L., Malone, D., Sotka, E. E. & Szmant, A. M. (1999) *Limnol. Oceanogr.* **44,** 1847–1861.

79. Hunter, C. L. & Evans, C. W. (1995) *Bull. Mar. Sci.* **57,** 501–515.
80. Bak, R. P. M., Lambrechts, D. Y. M., Joenje, M., Nieuwland, G. & Van Veghel, M. L. J. (1996) *Mar. Ecol. Prog. Ser.* **133,** 303–306.
81. Moran, P. J. (1986) *Oceanogr. Mar. Biol. Annu. Rev.* **24,** 379–480.
82. Bradbury, R. & Seymour, R. (1997) *Proc. 8th Int. Coral Reef Symp.* **2,** 1357–1362.
83. Turner, S. T. (1994) *Oceanogr. Mar. Biol. Ann. Rev.* **32,** 461–530.
84. Done, T. J. (1988) *Mar. Biol. (Berlin)* **100,** 51–61.
85. Sweatman, H. P. A. (1995) *Coral Reefs* **14,** 47–53.
86. Ayukai, T., Okaji, K. & Lucas, J. S. (1997) *Proc. 8th Int. Coral Reef Symp.* **1,** 621–626.
87. Wood, R. (1999) *Reef Evolution* (Oxford Univ. Press, Oxford).
88. Hallock, P. (1988) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **63,** 275–291.
89. Jackson, J. B. C. (1997) *Coral Reefs* **16,** Suppl., S23–S32.
90. May, R. M. (1977) *Nature (London)* **269,** 471–477.
91. Paine, R. T., Tegner, M. J. & Johnson, E. A. (1998) *Ecosystems* **1,** 535–545.
92. Nyström, M., Folke, C. & Moberg, F. (2000) *Trends Ecol. Evol.* **15,** 413–417.
93. Fabricius, K. E. & Wolanski, E. (2000) *Estuarine Coastal Shelf Sci.* **50,** 115–120.
94. Porter, J. W., Lewis, S. K. & Porter, K. G. (1999) *Limnol. Oceanogr.* **44,** 941–949.
95. Hughes, T. P. & Connell, J. H. (1999) *Limnol. Oceanogr.* **44,** 932–940.
96. Scheffer, M. (1990) *Hydrobiologia* **201,** 475–486.
97. Nee, S. & May, R. M. (1992) *J. Anim. Ecol.* **61,** 37–40.
98. Tilman, D., May, R. M., Lehman, C. L. & Novak, M. A. (1994) *Nature (London)* **371,** 65–66.
99. Stone, L. (1995) *Proc. R. Soc. London Ser. B* **261,** 381–388.
100. Stone, L., Eilam, E., Abelson, A. & Ilan, M. (1996) *Mar. Ecol. Prog. Ser.* **134,** 299–302.
101. Pandolfi, J. M. (1999) *Am. Zool.* **39,** 113–130.
102. Hanski, I. (1998) *Nature (London)* **396,** 41–49.
103. Mumby, P. J. (1999) *Mar. Ecol. Prog. Ser.* **180,** 275–288.
104. Jackson, J. B. C. (1986) *Bull. Mar. Sci.* **39,** 588–606.
105. Cowen, R. K., Lwiza, K. M. M., Sponaugle, S., Paris, C. B. & Olson, D. B. (2000) *Science* **287,** 857–859.
106. Jones, G. P., Milicich, M. J., Emslie, M. J. & Lunow, C. (1999) *Nature (London)* **402,** 802–804.
107. Swearer, S. E., Caselle, J. E., Lea, D. W. &Warner, R. R. (1999) *Nature (London)* **402,** 799–802.
108. Edinger, E. N. & Risk, M. J. (1994) *Palaios* **9,** 576–598.
109. Knowlton, N. & Weigt, L. A. (1998) *Proc. R. Soc. London Ser. B* **265,** 2257–2263.
110. Robertson, D. R. (1998) *Coral Reefs* **17,** 179–186.
111. Bellwood, D. R. (1997) *Proc. 8th Int. Coral Reef Symp.* **1,** 379–384.
112. Jackson, J. B. C., Winston, J. E. & Coates, A. G. (1985) *Proc. 5th Int. Coral Reef Congr.* **4,** 151–158.
113. Nee, S. & May, R. M. (1997) *Science* **278,** 692–694.
114. Johnson, K. G., Budd, A. F. & Stemann, T. A. (1995) *Paleobiology* **21,** 52–73.
115. White, A. T., Vogt, H. P. & Arin, T. (2000) *Mar. Pollut. Bull.* **40,** 598–605.
116. Tilman, D. & Lehman, C. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5433–5440.
117. Templeton, A. R., Robertson, R. J., Brisson, J. & Strasburg, J. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5426–5432.
118. Jackson, J. B. C. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5411–5418.
119. Jablonski, D. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5393–5398.
120. Erwin, D. H. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5399–5403.

Disrupting evolutionary processes: The effect of habitat fragmentation on collared lizards in the Missouri Ozarks

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Humans affect biodiversity at the genetic, species, community, and ecosystem levels. This impact on genetic diversity is critical, because genetic diversity is the raw material of evolutionary change, including adaptation and speciation. Two forces affecting genetic variation are genetic drift (which decreases genetic variation within but increases genetic differentiation among local populations) and gene flow (which increases variation within but decreases differentiation among local populations). Humans activities often augment drift and diminish gene flow for many species, which reduces genetic variation in local populations and prevents the spread of adaptive complexes outside their population of origin, thereby disrupting adaptive processes both locally and globally within a species. These impacts are illustrated with collared lizards (*Crotaphytus collaris*) in the Missouri Ozarks. Forest fire suppression has reduced habitat and disrupted gene flow in this lizard, thereby altering the balance toward drift and away from gene flow. This balance can be restored by managed landscape burns. Some have argued that, although human-induced fragmentation disrupts adaptation, it will also ultimately produce new species through founder effects. However, population genetic theory and experiments predict that most fragmentation events caused by human activities will facilitate not speciation, but local extinction. Founder events have played an important role in the macroevolution of certain groups, but only when ecological opportunities are expanding rather than contracting. The general impact of human activities on genetic diversity disrupts or diminishes the capacity for adaptation, speciation, and macroevolutionary change. This impact will ultimately diminish biodiversity at all levels.

Biodiversity has been defined at several levels of biological organization, including genes, species, communities, and ecosystems (1). Human activities are causing massive impacts on biodiversity at all these levels, but the impacts are most apparent to the general public at the species level and above as people witness loss of habitat, species extinction, disrupted communities, and polluted or otherwise damaged ecosystems. The impact of human activities on genetic diversity within a species is the least apparent and hence is often ignored. Genetic diversity is at the lowest hierarchy in this biodiversity sequence, which enhances—not diminishes—its importance. Without genetic diversity, a population cannot evolve, and it cannot adapt to environmental change. Environmental change is now occurring on a global scale because of human activities, and many species will have to adapt to this change or experience an ever-increasing chance of extinction. Moreover, as is common with many hierarchical systems, genetic diversity has an impact on the higher levels of biodiversity. Species, in their most basic sense, are evolving lineages (2–4), and the maintenance of their capacity to evolve requires the existence of genetic diversity (5). In this manner, species diversity emerges from genetic diversity over evolutionary time. Species diversity is seen in diversity of habitat needs and responses to other species. These species attributes in turn are the basis for much community and ecosystem structure. Hence, the impact of genetic diversity percolates through all levels of biodiversity via the evolutionary process.

Human activities can and do have dramatic effects on the amount and distribution of genetic diversity within species. As a consequence, human activities are directly altering the dynamics of evolution itself with respect to the fundamental evolutionary processes of adaptation and speciation. In this paper, examples are given of how human activities can disrupt the evolutionary potential for both adaptation and speciation.

Factors Controlling the Amount and Distribution of Genetic Variation Within Species

Genetic diversity is ultimately created by the process of mutation, which creates allelic diversity (alternative forms of genes at the same locus). This diversity is lost during the evolutionary process; some of it is lost at random (genetic drift in the species as a whole) and some because of natural selection (elimination of deleterious alleles and fixation of favorable alleles). The amount of allelic diversity in a species represents a dynamic balance among mutation, drift, and selection.

Species exist in both space and time, and so does intraspecific genetic diversity. In some species, allelic diversity is widely distributed across a species' entire geographical range, and all local populations contain virtually the same alleles and at similar allele frequencies. At the other extreme are species in which local populations have little or no internal allelic diversity, but different local populations can be fixed for alternative alleles. The forces that partition and create genetic hierarchies within a species are collectively known as population structure and include such factors as system of mating, genetic drift, and gene flow. The partitioning of allelic diversity within and among local breeding populations is primarily because of the dynamic balance between local genetic drift (which causes the local breeding population to lose allelic diversity but causes an increase in genetic differentiation among local populations) versus gene flow (which brings new allelic diversity into the local population and reduces genetic differentiation among populations). The allelic diversity within a reproducing population is translated into genotypic diversity through the mechanisms of gamete formation and gamete union (system of mating). During gamete formation, alleles at different loci are put together into various combinations by the processes of recombination and assortment, which greatly augments the potential for genotypic diversity. The

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Abbreviation: MDOC, Missouri Department of Conservation.

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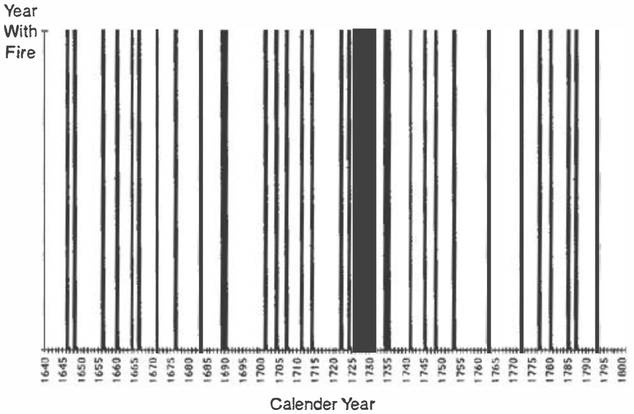

Fig. 1. The fire history of Stegall Mountain, as reconstructed from fire scars on stumps between 1640 and 1800.

system of mating determines the extent to which diploid individuals will themselves carry allelic diversity (in the form of heterozygosity).

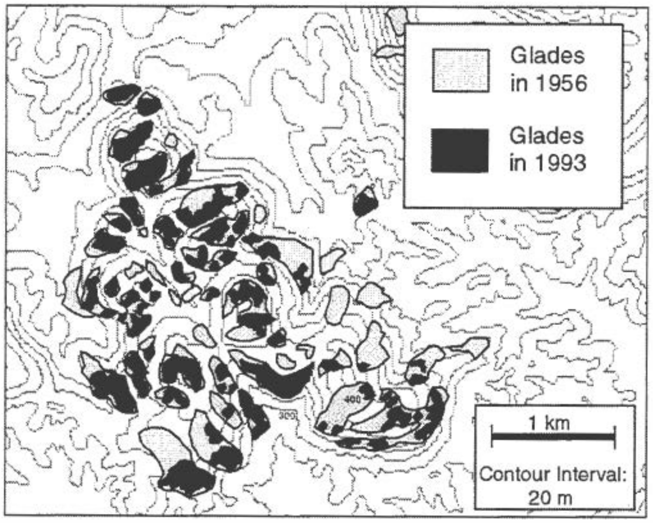

Fig. 2. Glade habitat on Stegall Mountain in 1956 versus 1993 as inferred from aerial photos.

Human-Induced Alterations in the Balance of Genetic Drift and Gene Flow

One of the primary impacts of many human activities is habitat fragmentation; that is, human use of the landscape creates habitat "islands", and the species within them often have little or no genetic contact with conspecific populations inhabiting other such islands. As an example, consider the eastern collared lizard (*Crotaphytus collaris collaris*), a species restricted to glades in the portion of its range located in the Ozarks. Ozark glades are barren, rocky outcrops, usually with a southern or southwestern exposure on a ridge top that creates a desert or dry prairie-like microhabitat (6). Desert-adapted plants and animals (such as scorpions, tarantulas, cacti, and collared lizards) invaded the Ozarks during the Xerothermic maximum about 8,000 years ago (the period of maximum warmth in our current interglacial period) and were cut off from their southwestern ancestral range at the end of the Xerothermic about 4,000 years ago (7). After that time and until European settlement, the fragmented Ozark glades were mostly separated by savannas—open mixed woodland and grassland areas (8, 9). Ozark savannas were a fire-maintained community, and before European settlement, fires occurred frequently in the Ozarks (10). For example, one of our field sites is in the Stegall Mountain Natural Area. Fig. 1 presents the fire history of this mountain from 1640 to 1800 as reconstructed from fire scar data on tree stumps (11, 12). As can be seen, the average interval between fires of sufficient intensity to produce fire scars was about once every 5 years, and no decade in this period had no fires. However, with European settlement, clear cutting occurred throughout most of the Ozarks, often followed by cutting of second-growth forest as well. The present forest grew during a time in which fires were suppressed, particularly from about 1950 to the present. This new forest is an oak–hickory forest with a dense understory. Although savanna was the dominant community type in the Ozarks in the early 1800s, less than 100 acres of it survived this replacement by the dense oak–hickory forest (13). In addition to changing the nature of the forest that separates the glades, the suppression of fire also allowed the invasion of glades by fire-sensitive eastern red cedars (*Juniperus virginiana*), which in turn allowed successional invasion by other woody species. As a consequence, many glades have been reduced in size, and some have disappeared completely (14). This destruction and increased fragmentation of glade habitats can be documented on Stegall Mountain by comparing a series of aerial photos taken in 1956 (graciously provided by the Missouri Department of Conservation) to a glade map of the same area from 1993 (Fig. 2).

These environmental changes had a drastic impact on the population structure of the collared lizard, particularly in the northeastern part of the Ozarks where European settlement first occurred. On the basis of microsatellite loci, the present populations have extreme population subdivision ($F_{ST} = 0.40$, which measures the proportion of the genetic variation in the *T*otal population that exists as differences between *S*ubpopulations), with little genetic diversity within any single glade population but many fixed genetic differences among even nearby glade populations (15, 16). This pattern indicates a combination of small local population sizes and little to no gene flow. The small population sizes are expected from the reduction in glade numbers and sizes and are confirmed by direct observations. For example, at Sandy Ridge, a glade with one of the more abundant and reliable collared lizard populations in the eastern Ozarks, the adult population size fluctuated between 21 and 79 individuals in the period 1975–1985 (O. Sexton, personal communication). Given that eigenvalue effective size (which measures the rate of loss of genetic variation) tends to be weighted most heavily by the smaller population size values when size fluctuates with time, the size fluctuations observed by Sexton imply that the Sandy Ridge population should be losing its genetic variation at a high rate. Most other glade populations in the northeastern Ozarks are even smaller. Hence, unless counteracted by gene flow, glade populations should experience intense genetic drift and an attendant loss of local population genetic variation. The genetic evidence indicates there is little to no gene flow among glade populations under present conditions. For example, fixed differences exist between populations separated by as little as 50 m of intervening forest (16). This lack of gene flow has also been confirmed by field experimentation. In 1983, in cooperation with the Missouri Department of Conservation (MDOC), we began a translocation program for collared lizards (17). The initial releases of translocated animals were made on glades at the Peck Ranch, a 23,000-acre wildlife area owned and managed by the MDOC that contains the Stegall Mountain Natural Area. This area had been ecologically devastated, first by extensive clear-cutting of its primary pine and oak woodlands in the 1800s, followed by clear-cutting of the secondary oak–hickory forest in the early 1900s and then by the raising of hogs and cattle on an open range. Protection of this area began in 1953, shortly after its purchase by the MDOC, and that protection included effective suppression of forest fires that unintentionally resulted in

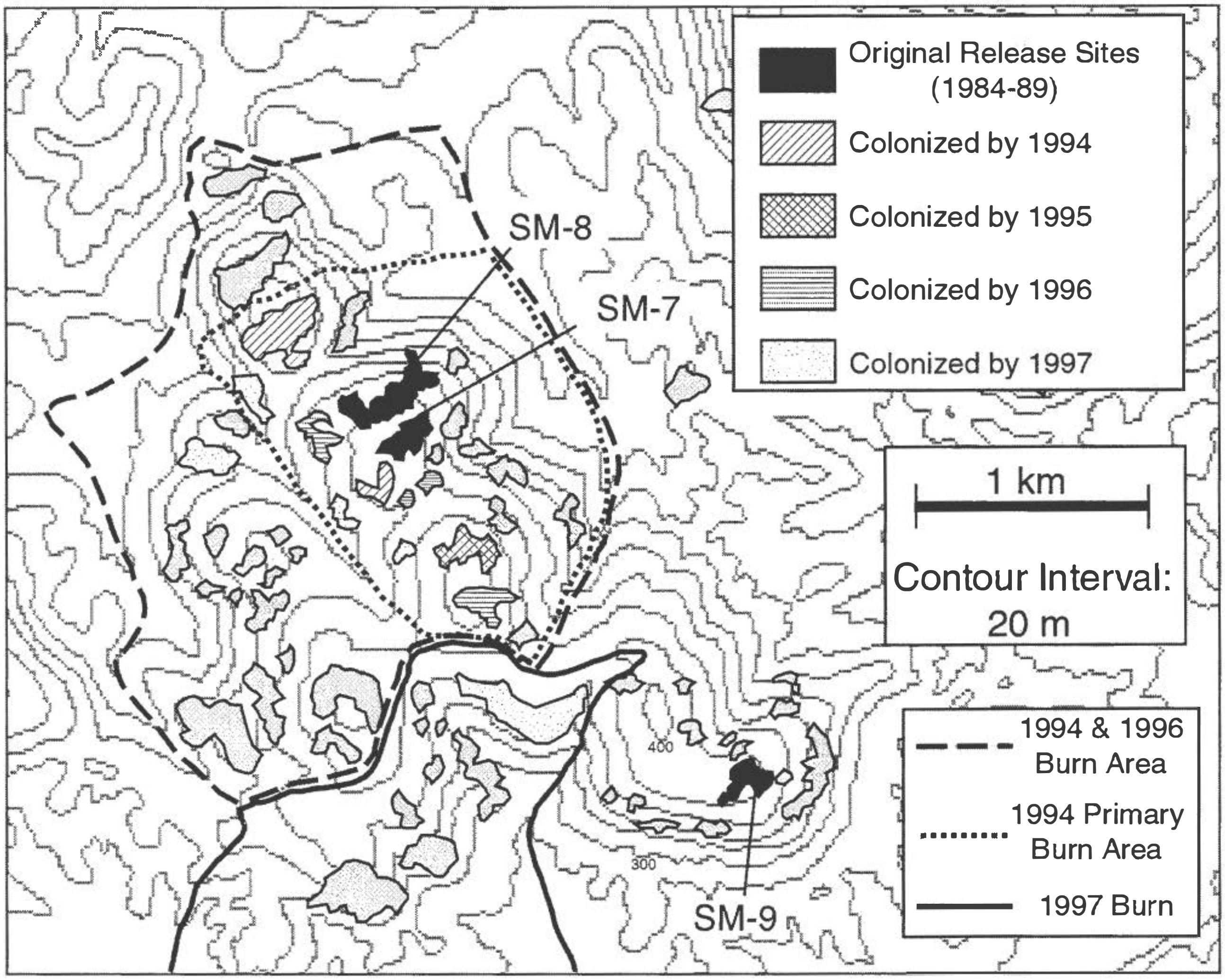

Fig. 3. Map of glades and burn areas on Stegall Mountain. The glades with areas filled in black were the sites of release of translocated collared lizard populations in 1984 (SM-7), 1987 (SM-8), and 1989 (SM-9). Different patterns within glades indicate the first year in which collared lizards were observed in that glade for the period 1984–1997.

extensive destruction and reduction of glade habitat (Fig. 2). Nothing is definitively known about collared lizard populations before 1980, but in that year, an extensive survey revealed that no collared lizard populations could be found on the Peck Ranch. Three populations were translocated onto glades on Stegall Mountain (Fig. 3), one each in 1984 (glade SM-7), 1987 (glade SM-8), and 1989 (glade SM-9). All three translocations were successful in the sense that the lizards were able to live and reproduce on these three glades. However, there was no gene flow or dispersal among these glades. Glades SM-7 and SM-8 are separated by only 50 m of intervening forest (Fig. 3), but despite annual observation trips, no animals were observed to have dispersed between them (on the basis of mark/recapture studies by using toe clipping to mark individuals) while the forest fire suppression policy was still in effect (up to and including 1993). Moreover, several empty glades existed in this area, the closest being only 60 m from glade SM-7. Several of these nearby glades were regularly monitored but were never colonized in the period 1984–1993. These monitoring studies support the inference from genetic data of little to no gene flow among the fragmented populations. Overall, this combination of low population sizes and no gene flow explains the high F_{ST} values observed in the northeastern Ozarks.

The genetic data also suggest that the lack of gene flow is a relatively recent phenomenon. First, within the northeastern Ozarks, there is no correlation between geographical distance with either pairwise F_{ST} values or their variances (15). This is the pattern one expects when a relatively genetically homogeneous ancestral population is suddenly fragmented into many small isolated units (15). The validity of this explanation can be tested directly by altering the fire regime once again. A Biodiversity Task Force assembled by the MDOC and the U.S. Forest Service made several management recommendations, including the use of managed forest fires on a landscape level (13). An initial fire management area was designated on Stegall Mountain (Fig. 3), although the first burn, in April 1994, was primarily confined to the northwestern portion of the designated burn area (Fig. 3). A subsequent burn in 1996 included the entire initial fire management area. In 1997, a second segment to the south of the 1994/1996 management area was burned (Fig. 3). As of 1999, all of the area shown in Fig. 3 and even beyond has been included in the fire management program, for a total of about 5,000 acres. After 1997, the situation with the lizards has become more complex and will require genetic testing in addition to mark/recapture data to sort out the dispersal among glades. These surveys are in progress, so for now we will confine our analysis to the initial response to the new forest fire management policy up to and including 1997.

These burns had a dramatic effect biologically. Three transects through the burned area set up and monitored by the MDOC

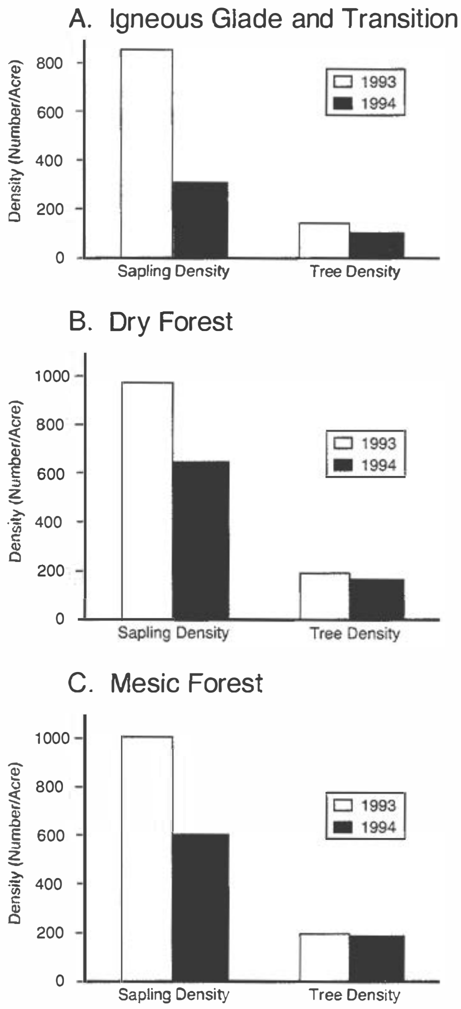

Fig. 4. Summary of three vegetation transects taken in 1993 (before the burn) and in 1994 (after the burn) in the fire management area on Stegall Mountain by the MDOC. The transects are subdivided into three major habitat types: (*A*) glades and the transitional areas between the glades and the dry forest; (*B*) dry forest; and (*C*) mesic forest.

revealed a marked change in woody vegetation (Fig. 4, on the basis of data kindly provided by T. Nigh and K. Kramer of the MDOC). The fire helped keep the glades clear of encroaching trees and saplings (Fig. 4 *Top*) and greatly altered the structure of the intervening forest. There was little impact on the canopy trees, but the understory was significantly thinned of saplings (Fig. 4 *B* and *C*) and became more open and dominated by grasses and herbaceous plants rather than woody species. The burns also had a dramatic effect on the population structure of the collared lizards.

The 1994 and 1996 burn areas include two glades on which collared lizards were translocated in 1984 and 1987 (SM-7 and SM-8, Fig. 3). A third glade, SM-9, was the site of a collared lizard release in 1989 but was outside the areas burned by 1997 (Fig. 3). Before 1994, a total of 63 lizards were marked on these 3 glades, and 9 were recaptured, all on the glade of original capture. Between 1994 and 1997, an additional 65 animals were marked in the burn area and 39 outside the burn area. Of 18 recaptures in the burn area, 9 represent dispersal events. Of 34 recaptures in the nonburned area, all 34 were on glade SM-9, the glade of initial capture. These data can be used to test the null hypothesis that burning does not affect dispersal, both temporally (before and after April 1994 in the burn area, Table 1) and spatially (after April 1994 in the burned versus unburned areas, Table 2). Table 1 reveals a highly significant ($P = 0.012$) change in dispersal rates before and after the 1994 burn within the initial fire management area. Table 2 reveals a highly significant ($P < 0.001$) difference in dispersal in the period 1994–1997 in the burned versus unburned portions of Stegall Mountain. Hence, interglade dispersal went from being nondetectable to being common in the areas that were burned.

Table 1. Recapture data on marked collared lizards in the areas burned between 1994 and 1997 on Stegall Mountain before (1984–1993) and after the burns (1994–1997)

Time period	Recaptured in glade other than glade of original capture	Recaptured in glade of original capture
1984–1993	0	9
1994–1994	9	9

A two-tailed Fisher's Exact Test is used to test the null hypothesis of no temporal effects. Two-tailed Fisher's Exact Test: $P = 0.012$.

The burns also had a significant impact on colonization rate. Before the 1994 burn, no glades had been colonized in the 10 summers that lizards were present in the area eventually burned. Between 1994 and 1997, 13 glades were colonized (Fig. 4), indicating a dramatic increase in colonization rate after the initiation of burning. Moreover, the colonization within burned areas has continued on Stegall Mountain, and 32 glades have been colonized between 1994 and 1999 versus no glades colonized between 1984 and 1993. For a spatial contrast, one glade was colonized in the unburned portion of Stegall between 1994 and 1997, whereas 12 were colonized in the burn area (Fig. 3). The one glade that was colonized in the unburned area actually shows the importance of clearing the understory for dispersal in this species. As can be seen from Fig. 2, glade SM-9 and the glade colonized in 1997 in the unburned area were originally part of a single large glade. In anticipation of extending the burn area to include this southwestern part of the main ridge of Stegall Mountain, during the winter of 1996/1997, MDOC workers cut with chain saws much of the woody vegetation that separated these two fragments of what was formerly a single glade. Although the population on glade SM-9 was very dense, no lizards colonized this nearby fragment between 1989 and 1996; they did so only after the clearing by chain saws. This 1997 colonization event indicates that the lizards' dispersal behavior is cued not by burning *per se* but rather by having an open understory. Therefore, the ability of collared lizards to disperse among and colonize glades depends strongly on the intervening forest structure, particularly the understory. These managed fires have established a gene flow and colonization regime today that is consistent with the inferred ancestral population structure before European settlement (15). Thus, human activities have had and continue to have a dramatic effect on gene flow in these lizard populations.

There have also been dramatic increases in population sizes after fire management. The founder population on Stegall

Table 2. Recapture data on marked collared lizards in the burned versus unburned areas between 1994 and 1997 on Stegall Mountain

Area	Recaptured in glade other than glade of original capture	Recaptured in glade of original capture
Unburned	0	34
Burned	9	9

A two-tailed Fisher's Exact Test is used to test the null hypothesis of no spatial effects. Two-tailed Fisher's Exact Test: $P < 0.001$.

Mountain consisted of 28 adult animals (10 on two glades and 8 on the third). Low recapture rates preclude a meaningful estimate of population size before the burns, but no obvious large increase in population size occurred at either of the glades in the area burned in 1994 and 1996, whereas the 1989 release population appeared to have achieved the greatest local population size, with 14 animals caught in 1993 on glade SM-9 in contrast to 4 apiece on glades SM-7 and SM-8 in 1993. In 1999, 233 individual animals were captured on Stegall Mountain, consisting of 107 adults and 126 hatchlings. This number of captures indicates at least a nearly 10-fold increase in population size from the original release population of 28 individuals, and the high percentage of hatchlings indicates a rapidly expanding population. Most of this increase in population size is attributable to the postburn colonization of 32 new glades. Moreover, the fires are increasing both the area and the quality of existing glades (Fig. 4 *Top*) and are allowing the colonization of small glades. For example, two of the glades colonized in 1996 lie well below the size range of 42 glades with natural populations of collared lizards in the northeastern Ozarks that we have surveyed since 1981. It is doubtful whether these small glades could maintain a viable population of collared lizards in isolation, but they are sufficiently large to provide good foraging territories for about two to five lizards. Now that lizards can disperse and are dispersing among glades, these small habitat islands are available for exploitation and help augment the total lizard population size. Interestingly, one of these smaller glades subsequently became unoccupied again, only to be recolonized later. Hence, metapopulation dynamics, defined by local extinctions and recolonizations, has now become established after the burns. Thus, the restoration of forest fires in this area has dramatically altered the balance between drift and gene flow in a manner that should maintain much higher levels of genetic diversity at the local glade population level and at the total Stegall Mountain population level (because of less overall genetic drift caused by dramatic increase in the total population size). Although the lizards still live in fragmented glade habitats, the extreme fragmentation induced by fire suppression has been replaced by frequent and effective gene flow among glade populations.

Disrupting the Evolutionary Potential for Adaptation

The balance between drift and gene flow and its impact on genetic variation in the local population's gene pool is important for three reasons: (*i*) the possibility that genetic uniformity makes populations more likely to experience high infection rates and rapid spreads of pathogens; (*ii*) the possibility that loss of local genetic diversity will reduce a population's ability to respond to environmental change through the process of adaptation; and (*iii*) the possibility that local adaptations will be unable to spread throughout the species from their local population of origin. Caro and Laurenson (18) questioned the importance of genetic variation with respect to increased risk to short-term extinction. (Note: Caro and Laurenson incorrectly state that it is loss of heterozygosity that may reduce a population's adaptive flexibility, but adaptive flexibility is bestowed by having genetic diversity in the gene pool—which may or not be in the form of heterozygosity at the diploid level.) Concerning point *i*, Caro and Laurenson (18) argue that the cases of increased epidemiological impact of pathogens in natural populations that are low in genetic variation are not definite proofs of the importance of genetic variation, although they are consistent with this conclusion (19, 20). However, the agricultural literature clearly shows the dangers of genetic monocultures with respect to pathogen epidemiology (21, 22). Given the consistency of the natural examples with agricultural work, it would be unwise to dismiss this role of genetic variation in mediating the intensity and ecological consequences of host/pathogen interactions. Greater epidemiological impact of pathogens can make it more likely that small local populations will go extinct—the ultimate disruption in evolutionary potential.

The lack of genetic diversity in local populations can disrupt adaptive evolution long before extinction. The need for genetic diversity as a prerequisite for adaptive evolution is well established theoretically and experimentally (e.g., ref. 23). There are also abundant natural examples of organisms using their genetic diversity to adapt to environmental, including human-induced, change (21). The importance of genetic diversity as a necessary component of adaptive evolution cannot be doubted, but adaptive flexibility is realized only over evolutionary time. Hence, the criterion of short-term extinction risk (18) is inherently an inappropriate criterion for assessing the importance of genetic diversity on adaptive flexibility. Moreover, the adaptive flexibility associated with high genetic diversity is typically interwoven with ecological conditions that also diminish extinction risk. For example, the collared lizards on Stegall Mountain now have the capacity to maintain high levels of genetic diversity available for local adaptation because of the larger population sizes and large amounts of gene flow that unite many glades into a single effective breeding population. The increased gene flow is caused by the lizards' ability to disperse through recently burned forests, which, as we have already noted, also allows colonization of unoccupied glades (another buffer against local extinction), including glades too small to support an isolated viable population (allowing increases in total population size, another powerful buffer against extinction). In general, the factors that promote increased genetic diversity for local populations also provide an ecological buffer against local extinction.

One area of potential confusion about the need for gene flow in facilitating local adaptive flexibility is Wright's shifting balance theory (24). Wright argued that restricted gene flow resulting in population subdivision creates the optimal conditions for adaptive breakthroughs. However, it would be a mistake to interpret the shifting balance theory as implying that human-induced fragmentation facilitates adaptation. Wright's shifting balance process requires gene flow to be restricted but not eliminated. With complete isolation of small local populations, the shifting balance process grinds to a halt for lack of variation within local populations. Moreover, recent theoretical and experimental work indicates that the shifting balance process works at higher levels of gene flow than Wright had first envisioned (25–29), and that it works with metapopulation structures with local extinction coupled with recolonization (30–32), as is now occurring with the collared lizards on Stegall Mountain. Thus, when gene flow is reduced to extremely low levels, as had occurred in the lizards during the period of forest fire suppression, even shifting balance ceases to contribute to adaptive change. Complete or nearly complete fragmentation therefore disrupts the process of local adaptation even under shifting balance.

Wright's shifting balance theory also emphasizes another important role for gene flow: the spread of an adaptive trait from its local population of origin to the remainder of the species (26, 27, 29, 33–35). This spread is called phase III of shifting balance and illustrates the importance of gene flow not only in local adaptation but also in global adaptation. As habitat fragmentation increases and severs gene flow, the spread of adaptive traits throughout a species becomes increasingly difficult, thereby disrupting global adaptation at the same time that local adaptive flexibility is diminished.

Disrupting the Evolutionary Potential for Speciation

It can be argued that although fragmentation disrupts adaptation, it may partially compensate in promoting biodiversity by facilitating the evolutionary process of speciation (ref. 1, p. 75). This idea is based on the idea of founder-induced speciation (36–40). Of these models, the theory of genetic transilience is not just a theory of how founder events can induce speciation but rather primarily of why the vast majority of founder events do *not* induce speciation (40). Very restrictive conditions must hold before a founder event is likely to trigger speciation (40), conditions of: innate properties (e.g., genomic recombination size, system of mating), historical properties (e.g., the nature of the ancestral population structure, founder numbers, the manner in which the founders were sampled), and ecological factors (the requirement for a rapid increase in population size shortly after the founder event). Recently there have been empirical tests of genetic transilience (41, 42), and the results have supported the predictions of genetic transilience theory, in its predictions both in factors favoring founder-induced speciation and those preventing such speciation (43, 44).

When conditions are favorable for genetic transilience, they can lead not only to explosive speciation rates but also to major adaptive breakthroughs and innovations and to the evolution of higher taxa. For example, the Hawaiian *Drosophila* have the right combination of innate and historical properties in an appropriate ecological context for genetic transilience (38). The Hawaiian *Drosophila* not only represent the most speciose group of *Drosophila*; they also display an extraordinary range of morphological, developmental, and ecological diversity for the genus as a whole and have led to the creation of new genera (45). The ecological context in this case consisted of the regular creation of new volcanic islands to serve as sites of colonization from the older islands. This ecological context creates a situation in which rare interisland founder events to newer islands should lead to explosive population growth after the founder event because of open ecological niches. Such rapid population growth shortly after the founder event is a critical and essential element to speciation via genetic transilience (40).

The requirement of rapid population growth immediately after the founder event means that founder events are likely to induce speciation only in environmental contexts of open or expanding ecological opportunities. However, the founder events induced by human fragmentation are often characterized by diminished, not enhanced, ecological opportunity. Consequently, we expect most human-induced fragmentation events to reduce genetic diversity and increase local extinction with no compensating facilitation of speciation. We know of no compelling examples, in either nature or the laboratory, of speciation via founder events without the flush phase of rapid population growth after the founder event.

Studies of the eastern collared lizard illustrate a fate of rapid local extinction after founder events induced by fragmentation. As noted above in our work on Stegall Mountain, under a fire regime, collared lizards successfully exploit small glade habitats as feeding and breeding territories. Once isolated (as they were when fires were suppressed), these small glade populations must inevitably go extinct. Since 1981, we have surveyed 130 glades in the northeastern Ozarks that had open areas that were as large as or larger than other nearby glades that had a population of collared lizards. Of these larger glades, collared lizard populations were still on 42 of them, indicating that 68% of these glades have experienced local extinction with no subsequent recolonization under the extreme fragmentation induced by fire suppression. This calculation assumes that all 130 glades had collared lizards before fire suppression occurred. In light of the fact that all these glades are close to a currently inhabited glade, this seems to be a reasonable assumption, given the results obtained at the Peck Ranch that lizards readily disperse to nearby glades when frequent fires occur. Indeed, we feel that this percentage is undoubtedly an underestimate of local extinction on larger glades, because we primarily surveyed areas with prior reports that collared lizards were present.

This local extinction process was directly observed for one glade, Victoria Glade. Because of its proximity to St. Louis, this glade has been included in a large number of scientific studies and is a common destination of field trips sponsored by Washington University and other local universities. As a consequence, there is excellent documentation of the plants and animals on this glade since the early 1950s. In the 1950s, this glade had a healthy population of collared lizards, but because of a lack of fire, eastern red cedars began to encroach on the glade, thereby destroying the open microhabitat essential for collared lizards. By 1962, the lizards had become extinct (O. Sexton, personal communication). In the 1980s, this glade was purchased in part by the MDOC and in part by The Nature Conservancy, both agencies initiating a management regime of clearing and burning (only the glade proper was initially burned and not the surrounding oak–hickory forest). By 1990, the glade had been returned to excellent condition (as judged by the plant community), but no collared lizards had recolonized the glade despite the existence of nearby natural populations on private property. Hence, fragmentation of the collared lizards in the eastern Ozarks has resulted in much local extinction without compensatory recolonization events. (This glade was subsequently recolonized by collared lizards, but only after fire management included the surrounding forest.) This situation resulted in an "extinction ratchet" (16, 46), in which each local extinction brings the total population closer and closer to global extinction. An extinction ratchet, not speciation, is the primary impact of human-induced fragmentation.

How to Prevent the Disruption of Evolutionary Processes

Under extreme fragmentation, adaptive potential is lost as the genetic diversity within local populations is eroded by genetic drift and lack of gene flow. The lack of gene flow also prevents the spread of adaptive genetic complexes. Speciation is unlikely in these fragmented isolates; rather, an extinction ratchet is created by the fragmentation. The rate at which this extinction ratchet operates is primarily a function of local, not global, population size. Similarly, the rate of erosion of genetic diversity within the isolates also depends on their local effective sizes. The dominance of local factors makes the erosion of genetic diversity and the extinction ratchet virtually unmanageable, as separate management efforts would be needed for each isolate. The only practical manner of dealing with the erosion of genetic diversity and the extinction ratchet is to reestablish landscape-level population dynamics. That is, we need to end the isolation, both genetic and ecological, of fragmented local populations.

This can be done. The Biodiversity Task Force for the State of Missouri (13) recommended that the goal of conservation policy should not be to preserve a list of species or communities that were present at some reference time; rather, we should be preserving the *processes* that underlie a dynamic biodiversity at all levels. The experiences at Stegall Mountain demonstrate that a reversal of fragmentation is possible when management focus shifts from lists of items to be preserved to fundamental evolutionary and ecological processes, and from local isolates to the landscape in which the isolates are imbedded. This landscape focus does not mean that all efforts focused on local isolates or specific species and communities must cease; these efforts often continue to be needed. Rather, if we truly want to avoid disrupting the evolutionary process and want to ensure healthy biodiversity at all levels, from the genetic up, we must add landscape-level process-oriented considerations to our conservation efforts.

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1. Meffe, G. K., Carroll, C. R. & Contributors (1997) *Principles of Conservation Biology* (Sinauer, Sunderland, MA).
2. Templeton, A. R. (1989) in *Speciation and Its Consequences,* eds. Otte, D. & Endler, J. A. (Sinauer, Sunderland, MA), pp. 3–27.
3. Templeton, A. R. (1998) in *Endless Forms: Species and Speciation*, eds. Howard, D. J. & Berlocher, S. H. (Oxford Univ. Press, Oxford), pp. 32–43.
4. Templeton, A. R. (1999) in *Evolutionary Theory and Processes: Modern Perspectives, Papers in Honour of Eviatar Nevo*, ed. Wasser, S. P. (Kluwer, Dordrecht, The Netherlands), pp. 171–192.
5. Templeton, A. R. (1981) *Annu. Rev. Ecol. Syst.* **12,** 23–48.
6. Nelson, P. & Ladd, D. (1981) *Missouriensis* **3,** 5–9.
7. Mondy, D. (1970) Master's thesis (Southern Illinois University, Edwardsville, IL).
8. Anderson, R. C. & Bowles, M. L. (1999) in *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*, eds. Anderson, R. C., Fralish, J. S. & Baskin, J. M. (Cambridge Univ. Press, Cambridge), pp. 155–170.
9. Heikens, A. L. (1999) in *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*, eds. Anderson, R. C., Fralish, J. S. & Baskin, J. M. (Cambridge Univ. Press, Cambridge), pp. 220–230.
10. Ladd, D. (1991) in *Proceedings of the Oak Woods Management Workshop* (Eastern Illinois University, Charleston, IL), pp. 67–80.
11. Batek, M. J., Rebertus, A. J., Schroeder, W. A., Haithcoat, T. L., Compas, E. & Guyette, R. P. (1999) *J. Biogeogr.* **26,** 397–412.
12. Guyette, R. & McGinnes, E. A., Jr. (1987) *Trans. Missouri Acad. Sci.* **16,** 85–93.
13. Nigh, T. A., Pflieger, W. L., Redfearn, P. L., Jr., Schroeder, W. A., Templeton, A. R. & Thompson, F. R., III (1992) *The Biodiversity of Missouri* (Missouri Department of Conservation, Jefferson City, MO).
14. Gerber, A. S. & Templeton, A. R. (1996) *Oecologica* **105,** 343–350.
15. Hutchison, D. W. & Templeton, A. R. (1999) *Evolution (Lawrence, Kans.)* **53,** 1898–1914.
16. Templeton, A. R., Shaw, K., Routman, E. & Davis, S. K. (1990) *Ann. Missouri Bot. Gard.* **77,** 13–27.
17. Templeton, A. R. (1996) in *Biodiversity in Managed Landscapes: Theory and Practice*, eds. Szaro, R. C. & Johnston, D. W. (Oxford Univ. Press, Oxford), pp. 315–325.
18. Caro, T. M. & Laurenson, M. K. (1994) *Science* **263,** 485–486.
19. O'Brien, S. J., Roelke, M. E., Marker, L., Newman, A., Winkler, C. A., Meltzer, D., Colly, L., Evermann, J. F., Bush, M. & Wildt, D. E. (1985) *Science* **227,** 1428–1434.
20. Moritz, C., McCallum, H., Donnellan, S. & Roberts, J. D. (1991) *Proc. R. Soc. London B* **244,** 145–149.
21. Bishop, J. A. & Cook, L. M. (1981) *Genetic Consequences of Man Made Change* (Academic, London).
22. Oldfield, M. L. (1984) *The Value of Conserving Genetic Resources* (U.S. Department of the Interior, National Park Service, Washington, DC).
23. Carson, H. L. (1961) *Evolution (Lawrence, Kans.)* **15,** 496–509.
24. Wright, S. (1932) *Proc. Sixth Int. Cong. Genet.* **1,** 356–366.
25. Bergman, A., Goldstein, D. B., Holsinger, K. E. & Feldman, M. W. (1995) *Genet. Res.* **66,** 85–92.
26. Kawata, M. (1999) *Evol. Ecol. Res.* **1,** 663–680.
27. Peck, S. L., Ellner, S. P. & Gould, F. (1998) *Evolution (Lawrence, Kans.)* **52,** 1834–1839.
28. Wade, M. J. & Goodnight, C. J. (1991) *Science* **253,** 1015–1018.
29. Wade, M. J. & Griesemer, J. R. (1998) *Am. Nat.* **151,** 135–147.
30. McCauley, D. E. (1993) *Oxford Surv. Evol. Biol.* **9,** 109–134.
31. Wade, M. J. & Goodnight, C. J. (1998) *Evolution (Lawrence, Kans.)* **52,** 1537–1553.
32. Wallace, B. (1992) *Genetica* **87,** 119–125.
33. Gavrilets, S. (1996) *Evolution (Lawrence, Kans.)* **50,** 1034–1041.
34. Moore, F. & Tonsor, S. J. (1994) *Evolution (Lawrence, Kans.)* **48,** 69–80.
35. Rogers, A. (1990) *Am. Nat.* **135,** 398–413.
36. Mayr, E. (1982) in *Mechanisms of Speciation*, ed. Barigozzi, C. (Liss, New York), pp. 1–19.
37. Mayr, E. (1954) in *Evolution as a Process*, eds. Huxley, J., Hardy, A. C. & Ford, E. B. (Princeton Univ. Press, Princeton, NJ), pp. 157–180.
38. Carson, H. L. & Templeton, A. R. (1984) *Annu. Rev. Ecol. Syst.* **15,** 97–131.
39. Carson, H. L. (1968) in *Population Biology and Evolution*, ed. Lewontin, R. C. (Syracuse Univ. Press, Syracuse, NY), pp. 123–137.
40. Templeton, A. R. (1980) *Genetics* **94,** 1011–1038.
41. Galiana, A., Moya, A. & Ayala, F. J. (1993) *Evolution (Lawrence, Kans.)* **47,** 432–444.
42. Rundle, H. D., Mooers, A. O. & Whitlock, M. C. (1998) *Evolution (Lawrence, Kans.)* **52,** 1850–1855.
43. Templeton, A. R. (1996) *Evolution (Lawrence, Kans.)* **50,** 909–915.
44. Templeton, A. R. (1999) *Evolution (Lawrence, Kans.)* **53,** 1628–1632.
45. Templeton, A. R. (1986) in *Evolutionary Processes and Theory*, eds. Karlin, S. & Nevo, E. (Academic, New York), pp. 497–512.
46. Templeton, A. R. (1982) *Nat. Areas J.* **2,** 35–38.

Colloquium

Human-caused environmental change: Impacts on plant diversity and evolution

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Human-caused environmental changes are creating regional combinations of environmental conditions that, within the next 50 to 100 years, may fall outside the envelope within which many of the terrestrial plants of a region evolved. These environmental modifications might become a greater cause of global species extinction than direct habitat destruction. The environmental constraints undergoing human modification include levels of soil nitrogen, phosphorus, calcium and pH, atmospheric CO_2, herbivore, pathogen, and predator densities, disturbance regimes, and climate. Extinction would occur because the physiologies, morphologies, and life histories of plants limit each species to being a superior competitor for a particular combination of environmental constraints. Changes in these constraints would favor a few species that would competitively displace many other species from a region. In the long-term, the "weedy" taxa that became the dominants of the novel conditions imposed by global change should become the progenitors of a series of new species that are progressively less weedy and better adapted to the new conditions. The relative importance of evolutionary versus community ecology responses to global environmental change would depend on the extent of regional and local recruitment limitation, and on whether the suite of human-imposed constraints were novel just regionally or on continental or global scales.

The earth is undergoing rapid environmental changes because of human actions (1–6). Humans have greatly impacted the rates of supply of the major nutrients that constrain the productivity, composition, and diversity of terrestrial ecosystems. Specifically, the natural rates of nitrogen addition and phosphorus liberation to terrestrial ecosystems (1, 7, 8) have been doubled, and atmospheric CO_2 concentrations have been increased to about 40% above preindustrial levels (9). Soil calcium levels are declining in some ecosystems because of increased rates of leaching caused by acidic deposition (10). Humans have relaxed biogeographic barriers to dispersal by accidentally or deliberately moving exotic species to new biogeographic realms (e.g., ref. 11). Through both active fire suppression and increased use of fire as a land clearing or management tool, humans have regionally changed fire frequency (12, 13), which is a major force structuring communities and ecosystems (14). Humans now appropriate more than a third of all terrestrial primary production (15), and, in doing so, have simplified or destroyed large portions of some types of ecosystems, leaving behind fragments that often lack herbivores or predators that provided important top-down constraints. Moreover, many human environmental impacts are projected to be two to three times stronger within 50 years (16). In total, humans may be imposing combinations of constraints that already do, or may soon, fall outside the ranges within which many species evolved.

Here we explore how and whether such changes could result in the loss of local diversity and accelerated extinction (3), and thus potentially decrease ecosystem functioning (e.g., refs. 17–19). The effects of environmental change on species composition, diversity, and ecosystem functioning are poorly understood. As a tool to explore this issue, we use theories that potentially can explain multispecies coexistence (20–29). These models are based on the interplay of environmental constraints and the trade-offs organisms face in dealing with these constraints. They can predict both the persistence of a large number of species (24–29) and the conditions that could lead to extinctions. Although mechanisms differ, all solutions to Hutchinson's (20) paradox of diversity have a similar structure (26, 28, 29). All mechanisms assume that two or more factors constrain fitness, and that intraspecific and interspecific trade-offs constrain each individual or species to having optimal performance at a particular value of these constraints. These processes provide a basis for interpreting the impacts of global human ecosystem domination on community composition, extinction, and speciation.

The physiology, morphology, and life history of a plant necessarily constrains it to survival in only a range of environmental conditions. In the classical literature, these conditions were called its fundamental niche. Each species is, at best, a superior competitor for a narrower range of conditions, classically called its realized niche (30–32). The attributes of sites and regions thus limit the types of species that can occur in them. These classical concepts of fundamental and realized niches underlie recent mechanistic approaches to competition, coexistence, and community structure (24, 25, 28, 33–36) and are a useful way to summarize natural history (e.g., refs. 37–39). Moreover, they suggest that human-caused environmental changes could create "vacant niches" (40)—i.e., evolutionarily novel suites of environmental conditions for which no species in a region are well adapted. In this paper, we use recent mechanistic theory to explore the potential impacts of human-driven environmental change on the composition and diversity of terrestrial plant communities, and on their patterns of speciation.

Environmental Constraints in Plant Communities

What are the major environmental variables that limit the abundance of terrestrial and aquatic plants, and which of these variables are being impacted significantly by human actions? In essence, plants may be limited by nutrients and other resources, by pathogens and herbivores, by disturbances, by dispersal abilities, and by the physical environment, including its climate. These constraints are elaborated below.

Resource Limitation. Plants require N, P, K, Ca, Mg, S, trace metals, CO_2, water, light, and other resources. Depending on the habitat and species, any one or several of these may be limiting. The most commonly limiting resources of terrestrial habitats are N, P, and water (24, 41–44). N limitation is common because the parent materials in which soils form contain almost no N.

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Rather, the chemically stable form of nitrogen is atmospheric N_2, which is usable only by N-fixing plants via microbial symbionts. Non-N-fixing plants obtain N as nitrate, ammonium, or organic N. Some soils are either initially low in other mineral elements, especially phosphorus and calcium, or become low in these after millennia of leaching. The Park Grass plots of Rothamsted, England have joint limitation by N, P, K, and early spring rainfall (43, 44). The greatest changes in plant community biomass, composition, and diversity came from N addition in the grasslands of both Rothamsted and Cedar Creek, Minnesota (45–47). Water is a limiting factor in many terrestrial habitats, as can be the atmospheric concentration of CO_2. Light may also be limiting, especially on productive soils in areas with low disturbance and low grazing rates.

Recruitment Limitation. All sessile plants have the potential to have their abundance limited by dispersal (25, 48–51). This occurs because dispersal is a neighborhood process, and because interspecific interactions also occur locally. Such "contact" processes can cause plants to have spatially patchy distributions (52), and thus to be missing from suitable habitat because of recruitment limitation. A one-time addition of seed of plant species that occurred in a savanna, but were absent from the local sites, led to an 83% increase in local plant species diversity and to a 31% increase in total community plant abundance (53). Because the added species occurred nearby, but were absent locally, their ability to germinate, grow, survive, and reproduce after a one-time seed addition showed that their abundance was limited by recruitment. Long-term observations in a Panamanian rainforest (51) also demonstrated strong recruitment limitation, as have seed addition experiments in other habitats (54, 55). Other evidence of dispersal limitation and of the rate of movement of plant species comes from studies of secondary succession. For instance, 10 to 15 years are required for *Schizachyrium scoparium*, a prairie plant that is a strong nitrogen competitor, to disperse from margins into abandoned fields, and another 30 years are required for it to attain peak abundance (46). This 40-year time delay between creation of a site and dominance is reduced to 3 years simply by adding seed of little bluestem. Cornell and Lawton (56) found that local diversity was limited less by local interspecific interactions than by recruitment from regional pools. Davis (57, 58) followed the dynamics of North American forests after glacial recession, and observed time lags of thousands of years between a region having the appropriate climate for a tree species and the arrival of that species. Such time lags could greatly influence responses of plant communities to human-caused environmental changes (58). Habitat fragmentation would lengthen such time delays.

Predators and Pathogens. Plant abundance in both terrestrial and aquatic ecosystems is also limited by the densities and species identities of pathogens and herbivores, which in turn can be limited both by their predators and by dispersal. Thus, top-down forces can greatly constrain both terrestrial and aquatic ecosystems.

Disturbance. Physical disturbances also limit terrestrial plant communities and sessile (benthic) freshwater and marine plant communities. For many terrestrial ecosystems, fire frequency has been a major constraint, as have been such physical disturbances as wind storms, landslides, mudslides, avalanches, clearings caused by gophers or other fossorial animals, disturbances caused by hooves, wallows, etc.

Temperature/Climate. The growth rates of terrestrial and aquatic plants are temperature-dependent, with species (and genotypes) having optimal growth and competitive ability at particular temperatures, and thus in particular climates. This is likely the greatest cause of the geographic separation of species along continental climatic gradients, such as north–south gradients and elevational gradients. In addition, the geographic ranges and abundance of many terrestrial plants are limited by temperature extremes, especially by tissue damage associated with freezing or subfreezing temperatures. In addition, within a region, differences in temperature-dependent growth could cause different plant species to be specialized on different portions of the growing season.

Temporal Variation. Plants respond not just to the mean levels of limiting factors, but also to the extent and patterning of their temporal variation. Some species may be limited or inhibited by such temporal variation, whereas other species may have traits that allow them to exploit such temporal variation (21, 22). This means that temporal variation, itself, can function as an additional limiting factor.

In total, there are a large number of factors and processes that constrain abundance of plants in both terrestrial and aquatic habitats. All of these limiting factors have been implicated as potential determinants of the species composition and diversity of various plant communities. Various combinations of two or, at times, three of these limiting factors have been formally incorporated into theories that are potentially capable of explaining the diversity and composition of terrestrial and aquatic plant communities. Changes in any of these constraints could thus change the abundance of species and genotypes in a habitat.

Anthropogenic Global Change and Plant Constraints

Many of these constraints are undergoing large, rapid changes because of human actions. Recent human activities have more than doubled the preindustrial rate of supply of N to terrestrial ecosystems (7). Nitrogen had a preindustrial terrestrial cycle that involved the annual fixation of about 90 to 140 Tg (teragrams) of N/yr (1, 7), with an additional 10 Tg of N/yr provided by atmospheric N fixation via lightening. Industrial N fixation for fertilizer currently totals about 88 Tg/yr. About 20 Tg/yr of N is fixed during the combustion of fossil fuels, and about 40 Tg/yr of N is fixed by legume crops. In addition, land clearing, biomass burning, and other human activities mobilize and release about an additional 70 Tg of N/yr. The projected expansion of global population to about 9 billion people by year 2050 and shifts to diets higher in animal protein suggest that, by 2050, global food production will be double its current rate (19). If so, anthropogenic terrestrial N inputs in 2050 would be about three to four times the preindustrial rate (16, 19). Much of this N would enter rivers and be carried to near-shore marine ecosystems. N would also be deposited atmospherically on nonagricultural terrestrial ecosystems

Nitrate is readily leached from soil, carrying with it positively charged ions such as Ca. Atmospheric N deposition may be depleting Ca and other cations in hardwood forests of the eastern United States (10). This depletion of base cations could cause elements that had not been limiting in a region to become limiting. Plant species often have distributions constrained by soil pH and Ca.

Phosphorus is a commonly applied agricultural fertilizer, and current P application is a doubling of the natural global rate for terrestrial ecosystems (8). Projections to year 2050 are that agricultural P fertilization will more than double. Much of this P may enter aquatic ecosystems, which can be P-limited.

The accumulation of such greenhouse gases as CO_2 and methane may lead to global climate change, with the greatest changes, especially warmer winter temperatures, forecast for temperate and polar ecosystems (e.g., ref. 2). Because climate change and its potential impacts on terrestrial ecosystems are widely studied, we will not review them here. Rather, we merely note that rainfall patterns, the frequency and severity of droughts, and other aspects of climatic mean and variance, which all constrain plant communities, are also forecast to change. In addition, CO_2 is a plant nutrient, and elevated levels of CO_2 represent atmospheric eutrophication with a limiting plant resource.

Fire frequency is a major variable controlling the species composition and diversity of forests and grasslands (e.g., ref. 14). In the United States, active fire suppression, habitat fragmentation, and other human activities have decreased by 10-fold the area burned each year, from about 22×10^6 ha/yr in 1930 to about 1.5×10^6 ha/yr since about 1960 (13). In contrast, fire frequency is greatly increasing in other habitats, especially tropical habitats, where fire is used as a land-clearing or land-management tool (59).

Modern transportation and commerce have immensely increased both accidental and deliberate introductions of species to novel biogeographic realms (11). About one quarter of the vascular plant species of California, for instance, are exotics. Exotic species are the second largest cause of native species of the United States being listed as endangered (60). Exotic species can impact the abundance of native species in a large number of ways, including via competitive suppression, via changes in disease incidence or some other trophic interaction, via inducing changes in the physical habitats, such as in fire frequency, and changes in nutrient cycles (61, 62). For instance, the invasion of the N-fixing *Myrica fava* into the Hawaiian Islands greatly increased local N fixation and thence soil N fertility. This increased soil fertility allowed other exotic species to increase in abundance once they were freed from N competition with native plants that where efficient N users (63).

Human actions have also fragmented habitats via conversion of native ecosystems to agricultural lands, urban or suburban lands, roads, power line rights-of-way, etc. Fragmentation is likely to escalate as population and per capita incomes increase globally. Habitat destruction can cause immediate extinction of those species that lived only in areas destroyed, and delayed extinction of poorly dispersing, perhaps competitively superior, species of extant ecosystems (64).

Finally, humans have decreased the geographic ranges and abundance of top predators, especially large carnivores. Decreased abundance of predators have had impacts in both aquatic and terrestrial habitats that have cascaded down the food chain (e.g., refs. 65 and 66), increasing abundance of some herbivores, decreasing abundance of their preferred plant species, and freeing herbivore-resistant species from competitive pressure.

In total, human actions are modifying many environmental constraints that, in combination with intraspecific and interspecific trade-off, led to the evolution of extant plant species and thus influenced the composition, diversity, and functioning of terrestrial and aquatic plant communities. If current trends continue, within 50 to 100 years the suites of factors constraining the structure of many plant communities may fall outside the envelope of values that existed both before the industrial revolution and when many of the plant species evolved.

Ecological Responses to Environmental Change

How would such changes in environmental constraints impact plant communities? Although there would be a continuum of responses, it is instructive to consider two ends of this spectrum: the more immediate, or "ecological" responses, and the more long-term, or "evolutionary" responses, especially patterns of speciation. Clearly, both ecological and evolutionary responses happen simultaneously. We separate them because the evolutionary response in which we are most interested is speciation, which is much slower than changes in species abundance. Ecological responses would depend on the constraints and trade-offs that had structured a given community and on how these had changed. Let us consider a case in which the composition and diversity of a plant community are determined by competition for nitrogen and light (e.g., ref. 28) and by dispersal limitation (25, 49), and explore the impacts of elevated N deposition. The qualitative changes that would occur in this plant community in response to elevated N deposition are the same as those that would occur in response to changes in any other environmental constraint.

Concepts and Theory. Assuming similar underlying physiologies, each plant species can be represented by the proportion of its biomass that is in either roots (for uptake of nitrogen), stem (which determines plant height and thus light capture), seed (which determines dispersal ability), or leaves (light capture via photosynthesis). For a given spatially homogeneous habitat—a site with a uniform soil of a given fertility (measured by the annual in-site mineralization rate of nitrogen)—and for a given physiology, there would be one pattern of biomass in root, stem, seed, and leaf that led to maximal competitive ability (28). On a low N soil, such as nutrient-maintained (rather than grazing-maintained) grasslands, the best competitor would have high root biomass, enough leaf biomass to provide photosynthate to meet the needs of roots, little biomass in stem (because light is not limiting), and little biomass in seed or rhizome. It would, in essence, be a short species that is an excellent N competitor but a poor disperser, perhaps much like the bunchgrass *S. scoparium* (little bluestem) of prairie grasslands on sandy soils in the United States, which are ecosystems that have historically experienced frequent burns. Plants with long-lived tissues, such as eracoids, might fill this role in less frequently burned habitats, because greater tissue longevity decreases plant N requirements (67).

Even if soils were spatially homogeneous, theory predicts that many other plant species could coexist with the best N competitor if they had appropriate trade-off between their competitive ability for N and their dispersal ability (23, 25, 27). Although there is an analytical limit to similarity for this mechanism of coexistence (25), there is no simple limit to the number of species that can stably coexist via this metacommunity process. This is the predominant mechanism of coexistence illustrated in Fig. 1*A*. It allows numerous species, each represented by a dot, to coexist with the major axis of differentiation being between root biomass (i.e., competitive ability for soil N) and seed biomass (i.e., dispersal ability). This defines the region of trait space in which species can coexist (28), which has a highly elongated shape (closed curve in Fig. 1*A*). This region of multispecies coexistence spans species with seed biomass from a few percent (the best competitor for N, which is more than 60% root) to more than 40% (the poorest competitor, but the best disperser). The region of coexistence includes species with different stem biomasses because of assumed spatial heterogeneity in the N content of soils. On more N rich soils, species with greater stem biomass are favored over those with more root biomass, because greater stem biomass allows better access to light. This, though, is a minor axis of coexistence compared with the seed–root trade-off for low N habitats.

A comparable pattern occurs for habitats with soils that have high N content (Fig. 1*B*). The elongated region of coexistence shown again represents coexistence mainly via a competition–colonization trade-off, but in this case the trade-off is between stem allocation (for light capture during competition for light) and seed allocation (dispersal ability that depends on the number and size of seed). Soils of intermediate fertility would favor species intermediate between the extremes shown in Fig. 1 *A* and *B*.

About a third of the globe has sandy soils with low N content. What would happen if a region with such soils were to receive

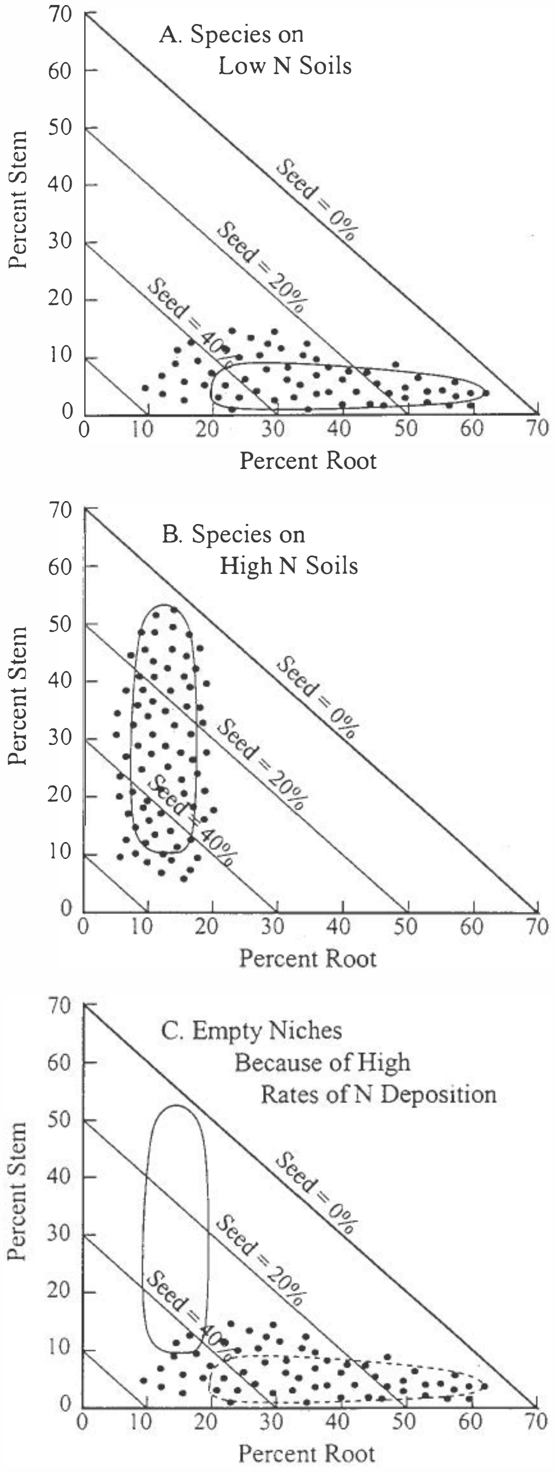

Fig. 1. (*A*) Plant species can be represented by the proportion of biomass in leaves, roots, stems, and seeds (28). In low nutrient habitats, superior competitors have high biomass in root, low biomass in stem and seed, and moderate biomass in leaves. Such superior competitors stably coexist with species that are progressively poorer competitors, but better dispersers (25). (*B*) In a fertile habitat, plant height and thus stem biomass is a determinant of competitive ability for light. (*C*) A nutrient-poor region, experiencing high rates of nutrient deposition. The region of coexistence includes only a few of the species originally present in the nutrient-poor region. These species would be competitively dominant and displace all of the other species, but be subject to invasion by species in the vacant region enclosed by the solid curve. Because Percent Root + Percent Stem + Percent Seed + Percent Leaf = 100%, Percent Leaf is about 30% for all cases shown.

projected increased rates of atmospheric N deposition? If all possible species were present throughout the region (i.e., if the whole triangular trait space of Fig. 1 were reasonably well covered with species), there would be a transition, as N accumulated, from a suite of species like those of Fig. 1*A* to a suite like that of Fig. 1*B*. However, given that the region receiving elevated N inputs started with low-N soil, the species of Fig. 1*B*, which occur on N-rich soils, would not be present. Rather, the responses observed would come from those species that happened to be present in the region—those shown in Fig. 1*A*.

The long-term response of this low-N habitat to greatly elevated N deposition should be dominance by superior light competitors, which have greater stem biomass. However, only two of the original species of the originally low N region would fall within the new trait space favored by N addition (Fig. 1*C*). These are both weedy species—i.e., species with high seed biomass compared with those that would be expected to be the competitive dominants of the elevated-N habitat. These species are favored initially because, of all of the species present in the original low-N habitat, they have relatively high stem biomass. Under conditions of elevated N, these two species would be expected to increase greatly in abundance where present and to rapidly spread to suitable sites because of their high seed biomass. Some of the other original species of the low-N community might coexist with them, if these additional species had the appropriate trade-off between their competitive ability for light and their dispersal ability. However, most species would be competitively displaced. Thus, a striking feature of Fig. 1*C* is that the vast majority of the species of the originally species-rich flora of this originally low N region would be competitively displaced by the new dominants. Thus, greatly elevated N deposition should lead to great local extinction.

A second striking feature is the extent to which there are "vacant niches" caused by environmental change—i.e., there are almost no species present in the regional flora that have traits that would normally be favored in such habitats. This is shown by the large empty area within the solid closed curve of Fig. 1*C*. Any species with traits that fell in this empty area should be able to invade into the region. In total, because of N deposition, the majority of the species that had been the dominants of a region when it was a low N habitat would be competitively displaced by a few formerly rare species, creating an ecosystem highly susceptible to invasion and species turnover until a community like that of Fig. 1*B* had developed.

Results of Experimental N Additions. Just such changes in plant diversity and composition are seen when one or a few such factors have been experimentally manipulated for extended periods of time. For instance, fertilization of the Park Grass plots with 4.8 g·m^{-2} of N, as ammonium sulfate, led to dominance by the grass *Agrostis* (84% of community biomass compared with an average abundance in unfertilized control plots of 12%) and to the loss of 14 of the 19 plant species found, on average, in unfertilized control plots (44, 68). The addition of 14.4 g·m^{-2} of N as ammonium sulfate together with P, K, Mg, and other nutrients led to extreme dominance by *Holcus lanatus* (Yorkshire fog, a grass), which had an average abundance of 96% in the two replicate high-N plots, compared with an average abundance in the three unfertilized and unlimed control plots of 2%. Both of the high-N plots contained only two plant species, whereas the controls averaged 19 plant species. Experimental N addition in a set of 207 grassland plots in Minnesota showed similarly strong loss of grassland species diversity and similar shifts in species composition at high rates of N addition (28, 69). Moreover, similar shifts in plant community diversity and composition have been reported for ecosystems experiencing high rates of atmospheric N deposition because of nearby intensive agriculture (70, 71). For instance, the heathlands of The Netherlands are an

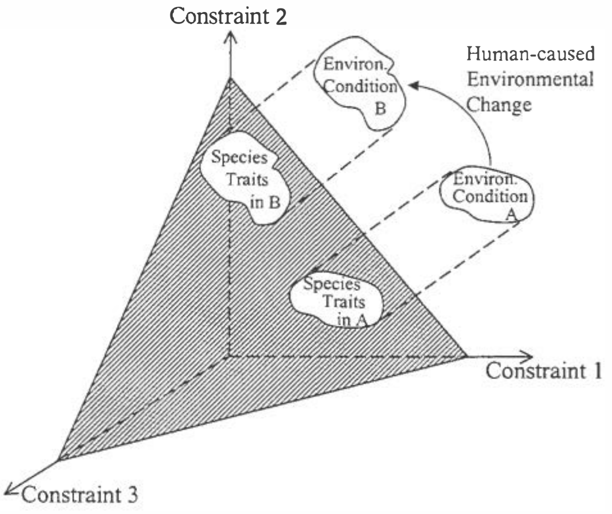

Fig. 2. The qualitative mapping of environmental conditions onto the traits of competitively superior species. The set of values of Constraints 1, 2, and 3 for Environmental Condition A, map into species traits on the trade-off surface, indicated by the shaded plane. Human-caused environmental change moves environmental conditions from Region A to Region B, causing a corresponding shift in the traits of the competitively dominant species.

ecosystem type that had dominated sandy soils for millennia. Agricultural intensification in The Netherlands in the 1960s and later was associated with high rates of N fertilization. Much of this N was first captured by crops, then entered cattle as feed, and later was volatilized as ammonia from their wastes. This led to about an order of magnitude increase in the rate of atmospheric N deposition, which contributed to the conversion of species-rich heathlands first into low-diversity stands of a weedy grass (*Molinia*) and then into shrubby forest (71).

A Generalization of Constraint Surfaces. These losses of diversity and shifts in species composition have, at their core, a conceptually simple basis (24, 44). The plant species that coexist in the unfertilized control plots do so for a variety of reasons, including interspecific trade-off in their ability to compete for limiting resources (e.g., ref. 24), or trade-off between competitive ability versus local dispersal ability (e.g., refs. 23, 25, and 27), or a trade-off between competitive ability versus resistance to herbivory or disease (e.g., refs. 24 and 72). If plant species coexist in the Park Grass plots because of competition for soil nutrients and light in a spatially heterogeneous environment (24), competitive abilities can be summarized by the relative shapes and positions of the resource-dependent growth isoclines of the species (24). Addition of N pushes this system toward an edge for which all plant species are limited by the same resource, light, and a single species is the superior competitor (24, 44). Moreover, the resource requirements of the Rothamsted species also depend on soil pH (24). The average soil pH of the unmanipulated Rothamsted soils was 5.3, whereas soil pH fell to 4.1 in the plot receiving 4.8 $g \cdot m^{-2}$ of N, and to 3.7 in the plots receiving 14.4 $g \cdot m^{-2}$ of N (68). In essence, the addition of the major limiting soil resource, N, and the associated shift to much more acidic soils, favored the plant species that could live in and were superior competitors for the novel conditions of high N, high plant biomass, low light penetration to the soil, and low soil pH.

Comparable patterns of dominance by a few formerly rare species, of competitive displacement of most existing species by these newly dominant species, and of high susceptibility to invasion by exotic species would be expected to occur for each of the types of human-caused changes in environmental constraints summarized above. In essence, a given habitat has various factors that constrain the fitness of the organisms that live there, and there is a trade-off surface that defines the potential responses (both within and among species) to these constraints (Fig. 2). Ecological processes, such as interspecific competition, map these environmental conditions onto the constraint surface and thus show the region of traits within which species must fall to persist in a region that has a given suite of environmental conditions (Fig. 2). Changes in any environmental conditions that limit organismal fitness, such as decreased fire frequency, increased N deposition, elevated CO_2, increased leaching loss of Ca and P, decreased herbivory, etc., would move the region of coexistence, as illustrated in Fig. 2.

The High Dimensionality of Environmental Change. The greater the dimensionality of a habitat is (i.e., the greater its number of constraints), the more its diversity and composition would be impacted by a given amount of environmental change in each variable. As reviewed above, human actions are changing many environmental constraints simultaneously, including N, P, Ca, CO_2, pH, fire frequency, trophic structure, and climate. The high dimensionality of these changes may lead to much greater impacts on plant communities than anticipated from a consideration of only one or a few of these factors.

A simple example illustrates this. Consider a habitat in which there are three constraints, factors 1, 2, and 3. The low and high values of these factors might map into a cubic trait space for competitive coexistence. If the values of factor 1 were shifted up by 50%, but nothing else changed, the old trait space and the new trait space would share 50% of their volume, indicating that this change would eliminate about half of the original species and create vacant niches that could be colonized by a comparable number of species, should they exist regionally. If both factor 1 and 2 were increased 50%, the new trait space would overlap with only 25% of the old (i.e., $1/2 \times 1/2 = 1/4$). If each of the three factors were shifted by 1/2, new trait space would overlap with only 1/8 of the original. In this case, 7/8 of the original species would be driven locally extinct. Comparably, if each of three variables were to be shifted by 2/3, the resultant trait space would overlap only 1/27 of its original volume, and 26/27 of the original species would be lost, on average.

A more formal, although still highly abstracted, treatment of this matter can be provided by a simple extension of Hutchinson's (30) abstraction of the niche as a hypervolume. Suppose species abundance is limited by multiple environmental factors defining orthogonal niche axes and forming a niche space whose boundaries are determined by the largest and smallest possible values of the environmental factors. Suppose that physiological and morphological trade-offs, as well as adaptation to past interspecific interactions, imply some optimal point in the niche space at which the species performs best, and away from which performance drops off. In two dimensions, for example, the axes might be soil pH and temperature, and performance might drop off as in a bivariate normal surface whose peak is at the optimal point (19). In a discrete approximation, the bivariate normal surface becomes a circle within which the species can survive, outside of which it cannot. In multiple dimensions, the circle becomes a hypersphere.

In this abstract view of the niche, prevailing environmental conditions are points in the niche space, and if the species can survive in the prevailing environment, those points fall within the species' niche hypersphere. Anthropogenic actions that change environmental conditions move those points to new locations in the niche space. What is the chance that the moved points will fall within the hypersphere of the species?

With random and independent changes, that chance can be calculated simply by dividing the volume of the species' niche hypersphere by that of the entire niche space. Assuming the species niche is smaller than the entire niche space, then using formulae for the volumes of n-dimensional hyperspheres and hypercubes, that chance can be shown to be always less than

$$2^{-n}\pi^{n/2}/(n/2)!\,,$$

where n is the number of environmental conditions changed, and where the factorial is computed via the gamma function when n is odd. Under these assumptions, if two environmental conditions were changed ($n = 2$), at most about 80% of the species on average would survive, but if eight conditions were changed randomly at once, at most about 1% of the species on average would survive. This multiplicative effect of changes in limiting factors means that several small changes can have as great an impact as one larger change, and that various combinations of small and large environmental changes can, in combination, have an immense impact. Thus, the ecological impacts of human-caused environmental change should depend on the dimensionality of the suite of factors that constrain species abundance, and, in a multiplicative manner, on the magnitudes of changes in all these factors.

In the short-term, such shifts in environmental constraints would eliminate many species and favor once-rare species. The longer-term dynamics of these terrestrial plant communities would depend on the dispersal rates of species both within a region and from other regions, if any, that formerly had characteristics similar to those that occur in the human-impacted region. They also would depend on the evolutionary responses of the species that remain in these habitats.

Evolutionary Responses to Global Change

What might the long-term outcome be of evolution under novel environmental conditions? For one possibility, let us consider again, but on an evolutionary time scale, the effects on a low-N terrestrial plant community of a large increase in the regional rate of N deposition. This could cause light and dispersal ability to become major limiting factors, as illustrated in Fig. 1*C*. As already discussed, the immediate effect of a high rate of N deposition would be dominance by a few formerly rare, fast-growing, rapidly dispersing plant species. These species would rapidly spread and overtop low-N-adapted species and thus out-compete them for light. However, a large portion of the viable trait space of this community would be empty, as in Fig. 1*C*. Assuming that N deposition is occurring on a geographically large region, or that habitat fragmentation or other dispersal barriers prevent colonization by suitable superior light competitors, or that the region has experienced other environmental changes (e.g., Ca leaching, soil acidification, invasion by pathogens) that make it inhospitable for otherwise suitable superior light competitors, its longer-term dynamics would be driven as much, or more, by internal evolutionary processes than by colonization.

The evolutionary dynamics of such systems have been explored for situations in which it is assumed that there is a strict trade-off between competitive ability and dispersal ability (36, 73, 74). Let us ask what might happen to a weedy plant species that was the initial dominant of a formerly N-poor habitat that experienced elevated N deposition, as shown in Fig. 1*C*. Numerical solutions to a partial differential equation model (36) show that, within the initially dominant weedy species (species 1 of Fig. 3*A*), those individuals that are better light competitors have greater fitness than those that are better dispersers. This causes the weedy species to evolve into a progressively better light competitor (acquiring such traits as a larger proportion of biomass in stem, greater height, and larger seed), but to produce fewer seeds and/or allocate less to vegetative spread. Thus, species 1 evolves to the right in Fig. 3*A*. As species 1 evolves into a better local competitor (and thus a poorer disperser), it occupies fewer sites in the spatial habitat. After this has progressed sufficiently far, an interesting phenomenon occurs. Individuals at the far end of the range of phenotypes, which are good dispersers but poor light competitors, are also favored (species 2 of Fig. 3*B*). These individuals are poor light competitors, and thus do not competitively inhibit species 1. However, they are good dispersers, which allows them to live in the sites not occupied by species 1.

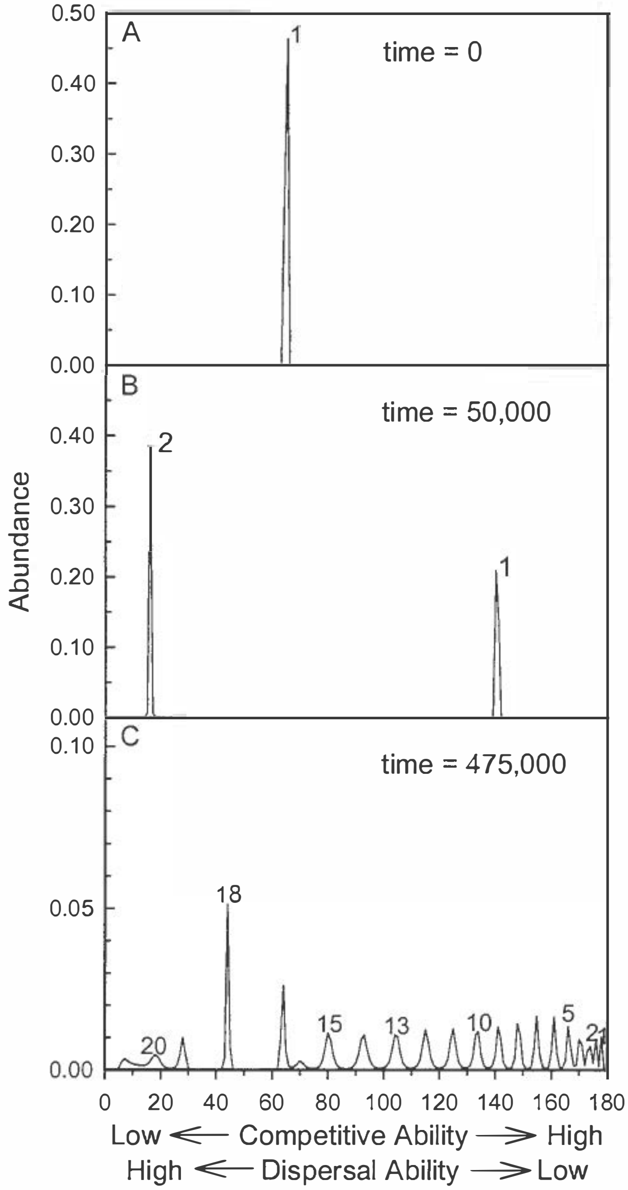

Fig. 3. Numerical solutions of evolutionary change in a weedy species growing in a spatially implicit habitat in which fitness is limited both by dispersal ability and by competitive ability, based on a model of phenotypic diffusion (36). (*A*) Given this trade-off, an initially weedy species, species 1, undergoes evolutionary change, with its peak shown moving to the right. (*B*) After 50,000 years, species 1 has evolved into a much better competitor, but a much poorer disperser than it originally was, and a new species, species2, has appeared. Species 2 is a superior disperser, but an inferior competitor. It survives in vacant sites in this spatial habitat. (*C*) Species 1 and 2 each evolve toward being superior competitors. After some time a third species appears that is a poor competitor, but excellent disperser. This third species evolves into a superior competitor and a fourth species appears, etc. Shown here is the result after 475,000 years, at which time 21 peaks of abundance appear, each peak representing a different phenotype, thus corresponding with different species.

In essence, there is a bimodal selective pressure created by competition in a spatial habitat and by an analytical limit to similarity for coexistence of organisms with traits at different points on the trade-off curve (36). This leads to two peaks on the trade-off curve, each peak corresponding to an incipient species (Fig. 3*B*). Such peaks appear even when all phenotypes are initially rare, and result from the interplay of selection, mutation/recombination, and the competitive limit to similarity. Within each of these peaks, those individuals that are superior light competitors but inferior dispersers are favored, causing the peaks to move to the right in Fig. 3*B*. Once the second peak, incipient species 2, moves sufficiently far to the right, a third peak appears. It also evolves toward the right, and a fourth peak appears, etc. In numerical solutions of the underlying reaction-diffusion model, after a 475,000 year period, a single weedy species had speciated into 21 species (Fig. 3*C*) that spanned the empty niche space of Fig. 1*C*. Such speciation processes would occur within each of the original weedy species, and eventually would yield a local flora as species-rich as occurred before N deposition.

In total, this process suggests that the imposition of novel environmental constraints would lead to the eventual diversification of the flora of a region, with the new flora filling in the empty niches created by novel human-caused environmental conditions. The process by which this is predicted to occur is one in which the ancestral progenitors of this new flora are small, fast-growing, weedy species. Interestingly, this is just what has been suggested to have occurred during the evolution of the angiosperms, during diversification in corals, and during the diversification of terrestrial mammals.

Conclusions

Anthropogenic changes in environmental limiting factors are likely to cause significant loss of plant diversity, leaving many niches empty and creating plant communities dominated by weedier species (poor competitors but good dispersers). The extent of this effect will depend both on the number of constraints that are changed (i.e., dimensionality) and on the magnitude of such changes. Because the impact of multidimensional environmental changes are expected to be multiplicative, a series of relatively small changes may be as important as a single major change. The vacant niches of a region experiencing a major change in an environmental constraint, such as a high rate of N deposition (Fig. 1*C*), indicate several things about such habitats. First, species that have traits that fall within the newly created vacant niches should be able to invade into, spread through, and persist if propagules are regionally available. Secondly, any heritable variation within existing species that allowed individuals to fill the vacant niches would be favored. For instance, following N deposition, there would be especially strong selection favoring those individuals with greater competitive ability for light, even if this cost dispersal ability. Until the available genetic variation for such traits was consumed, such evolution would be rapid. However, it seems unlikely that such species could rapidly evolve to be equivalent to the species of habitats that had a long evolutionary history of nitrogen rich soils. As such, these newer systems might long be susceptible to invasion by such species, with such invasion often leading to the displacement of the species that were evolving *in situ*.

Clearly, all of the ideas we have discussed are speculative extensions of a few simple models of community structure and assembly. Such models merit further testing and deeper exploration of their ecological and evolutionary implications.

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1. Vitousek, P. M. (1994) *Ecology* **75,** 1861–1876.
2. Houghton, J. T., Meiro Filho, L. G., Callandar, B. A., Harris, N., Kattenberg, A. & Maskell, K. (1996) *Climate Change 1995: The Science of Climate Change* (Cambridge Univ. Press, Cambridge, U.K.).
3. Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. (1995) *Science* **269,** 347–350.
4. Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. (1997) *Science* **277,** 494–499.
5. Matson, P. A., Parton, W. J., Power, A. G. & Swift, M. J. (1997) *Science* **277,** 504–509.
6. Tilman, D. (1999) *Proc. Natl. Acad. Sci. USA* **96,** 5995–6000.
7. Vitousek, P. M., Aber, J. D., Howarth, R. W., Likens, G. E., Matson, P. A., Schindler, D. W., Schlesinger, W. H. & Tilman, D. (1997) *Ecol. Appl.* **7,** 737–750.
8. Carpenter, S. R., Caraco, N. F., Correll, D. L., Howarth, R. W., Sharpley, A. N. & Smith, V. H. (1998) *Ecol. Appl.* **8,** 559–568.
9. Schlesinger, W. H. (1997) *Biogeochemistry: An Analysis of Global Change* (Academic, San Diego).
10. Likens, G. E., Driscoll, C. T., Buso, D. C., Siccama, T. G., Johnson, C. E., Lovett, G. M., Fahey, T. J., Reiners, W. A., Ryan, D. F., Martin, C. W., *et al.* (1998) *Biogeochemistry* **41,** 89–173.
11. Lonsdale, W. M. (1999) *Ecology* **80,** 1522–1536.
12. Bird, M. I. & Cali, J. A. (1998) *Nature (London)* **394,** 767–769.
13. Tilman, D., Reich, P., Phillips, H., Menton, M., Patel, A., Vos, E., Peterson, D. & Knops, J. (2000) *Ecology* **81,** 2680–2685.
14. Clark, J. S. (1990) *Ecol. Monogr.* **60,** 135–159.
15. Vitousek, P. M., Ehrlich, P. R., Ehrlich, A. H. & Matson, P. A. (1986) *Bioscience* **36,** 368–373.
16. Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W., Simberloff, D. & Swackhamer, D. (2001) *Science* **292,** in press.
17. Chapin, F. S., III, Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., *et al.* (2000) *Nature (London)* **405,** 234–242.
18. Tilman, D. & Downing, J. A. (1994) *Nature (London)* **367,** 363–365.
19. Tilman, D. (1999) *Ecology* **80,** 1455–1474.
20. Hutchinson, G. E. (1961) *Am. Nat.* **95,** 137–147.
21. Armstrong, R. A. & McGehee, R. (1980) *Am. Nat.* **115,** 151–170.
22. Levins, R. (1979) *Am. Nat.* **114,** 765–783.
23. Horn, H. S. & MacArthur, R. H. (1972) *Ecology* **53,** 749–752.
24. Tilman, D. (1982) *Resource Competition and Community Structure. Monographs in Population Biology* (Princeton Univ. Press, Princeton).
25. Tilman, D. (1994) *Ecology* **75,** 2–16.
26. Tilman, D. & Pacala, S. (1993) in *Species Diversity in Ecological Communities*, eds. Ricklefs, R. E. & Schluter, D. (Univ. of Chicago Press, Chicago), pp. 13–25.
27. Hastings, A. (1980) *Theor. Popul. Biol.* **18,** 363–373.
28. Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities* (Princeton Univ. Press, Princeton).
29. Chesson, P. & Huntly, N. (1997) *Am. Nat.* **150,** 519–553.
30. Hutchinson, G. E. (1957) *Quant. Biol.* **22,** 415–427.
31. MacArthur, R. H. (1968) in *Population Biology and Evolution*, ed. Lewontin, R. C. (Syracuse Univ. Press, Syracuse, NY), pp. 159–176.
32. Whittaker, R. H. & Levin, S. A., eds. (1975) *Niche: Theory and Application, Benchmark Papers in Ecology* (Halsted Press, Stroudsburg, PA).
33. Maguire, B. (1973) *Am. Nat.* **107,** 213–246.
34. Van den Bergh, J. P. & Braakhekke, W. G. (1978) in *Structure and Functioning of Plant Populations*, eds. Freysen, A. H. J. & Woldendorp, J. W. (North Holland Publishing Co., Amsterdam), pp. 125–138.
35. Comins, H. N. & Noble, I. R. (1985) *Am. Nat.* **126,** 706–723.
36. Lehman, C. & Tilman, D. (1997) in *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*, eds. Tilman, D. & Kareiva, P. (Princeton Univ. Press, Princeton), pp. 185–203.
37. Cody, M. L. (1986) in *Community Ecology*, eds. Diamond, J. & Case, T. (Harper and Row, New York), pp. 381–405.
38. Grubb, P. J. (1977) *Biol. Rev.* **52,** 107–145.
39. Chesson, P. (1991) *Trends Ecol. Evol.* **6,** 26–28.
40. Lawton, J. H. (1984) in *Ecological Communities: Conceptual Issues and the Evidence*, eds. Strong, D. R., Simberloff, D., Abele, L. G. & Thistle, A. B. (Princeton Univ. Press, Princeton), pp. 67–100.
41. Vitousek, P. (1982) *Am. Nat.* **119,** 553–572.
42. Vitousek, P. M. (1984) *Ecology* **65,** 285–298.
43. Thurston, J. M., Williams, E. D. & Johnston, A. E. (1976) *Annales Agronomiques* **27,** 1043–1082.

44. Tilman, D., Dodd, M. E., Silvertown, J., Poulton, P. R., Johnston, A. E. & Crawley, M. J. (1994) in *Long-term Experiments in Agricultural and Ecological Sciences*, eds. Leigh, R. A. & Johnston, A. E. (CAB International, Wallingford, Oxon, U.K.), pp. 287–303.
45. Tilman, D. (1987) *Ecol. Monogr.* **57,** 189–214.
46. Tilman, D. (1990) *Oikos* **58,** 3–15.
47. Wedin, D. A. & Tilman, D. (1996) *Science* **274,** 1720–1723.
48. Platt, W. & Weis, I. (1977) *Am. Nat.* **111,** 479–513.
49. Hurtt, G. C. & Pacala, S. W. (1995) *J. Theor. Biol.* **176,** 1–12.
50. Chesson, P. (1998) *Aust. J. Ecol.* **23,** 234–240.
51. Hubbell, S. P., Foster, R. B., O'Brien, S. T., Harms, K. E., Condit, R., Wechsler, B., Wright, S. J. & Loo de Lao, S. (1999) *Science* **283,** 554–557.
52. Durrett, R. & Levin, V. (1994) *Theor. Popul. Biol.* **46,** 363–394.
53. Tilman, D. (1997) *Ecology* **78,** 81–92.
54. Cavers, P. B. & Harper, J. L. (1967) *J. Ecol.* **55,** 59–71.
55. Robinson, G. R., Quinn, J. F. & Stanton, M. L. (1995) *Ecology* **76,** 786–794.
56. Cornell, H. V. & Lawton, J. H. (1992) *J. Anim. Ecol.* **61,** 1–12.
57. Davis, M. B. (1981) in *Forest Succession*, eds. West, D. C., Shugart, H. H. & Botkin, D. B. (Springer, New York), pp. 132–153.
58. Davis, M. B. (1986) in *Community Ecology*, eds. Diamond, J. & Case, T. (Harper and Row, New York), pp. 269–284.
59. Goldammer, J. G. (1991) in *Global Biomass Burning: Atmospheric, Climatic, and Biospheric Implications*, ed. Levine, J. S. (MIT Press, Cambridge, MA), pp. 83–91.
60. Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) *Bioscience* **48,** 607–615.
61. Walker, L. R. & Smith, S. D. (1997) in *Assessment and Management of Plant Invasions*, eds. Luken, J. O. & Thieret, J. W. (Springer, New York), pp. 69–86.
62. Mack, M. C. & D'Antonio, C. M. (1998) *Trends Ecol. Evol.* **13,** 195–198.
63. D'Antonio, C. M. & Vitousek, P. M. (1992) *Annu. Rev. Ecol. Syst.* **23,** 63–87.
64. Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. (1994) *Nature (London)* **371,** 65–66.
65. Ellenberg, H. (1988) *Vegetation Ecology of Central Europe* (Cambridge Univ. Press, Cambridge, U.K.), 4th Ed.
66. Carpenter, S. R. & Kitchell, J. F. (1993) *The Trophic Cascade in Lakes* (Cambridge Univ. Press, Cambridge, U.K.).
67. Chapin, F. S., III. (1980) *Annu. Rev. Ecol. Syst.* **11,** 233–260.
68. Williams, E. D. (1978) *Botanical composition of the Park Grass plots at Rothamsted 1856–1976* (Rothamsted Experimental Station, Harpenden, Herts, England).
69. Tilman, D. (1996) *Ecology* **77,** 350–363.
70. Berendse, F. & Aerts, R. (1984) *Acta Ecologica* **5,** 3–14.
71. Aerts, R. & Berendse, F. (1988) *Vegetatio* **76,** 63–69.
72. Levin, B. R., Stewart, F. M. & Chao, L. (1977) *Am. Nat.* **111,** 3–24.
73. Kinzig, A. P., Levin, S. A., Dushoff, J. & Pacala, S. (1999) *Am. Nat.* **153,** 371–383.
74. Lehman, C. (2000) Ph.D. Thesis (Univ. of Minnesota, St. Paul).

Colloquium

Plant biology in the future

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In the beginning of modern plant biology, plant biologists followed a simple model for their science. This model included important branches of plant biology known then. Of course, plants had to be identified and classified first. Thus, there was much work on taxonomy, genetics, and physiology. Ecology and evolution were approached implicitly, rather than explicitly, through paleobotany, taxonomy, morphology, and historical geography. However, the burgeoning explosion of knowledge and great advances in molecular biology, e.g., to the extent that genes for specific traits can be added (or deleted) at will, have created a revolution in the study of plants. Genomics in agriculture has made it possible to address many important issues in crop production by the identification and manipulation of genes in crop plants. The current model of plant study differs from the previous one in that it places greater emphasis on developmental controls and on evolution by differential fitness. In a rapidly changing environment, the current model also explicitly considers the phenotypic variation among individuals on which selection operates. These are calls for the unity of science. In fact, the proponents of "Complexity Theory" think there are common algorithms describing all levels of organization, from atoms all the way to the structure of the universe, and that when these are discovered, the issue of scaling will be greatly simplified! Plant biology must seriously contribute to, among other things, meeting the nutritional needs of the human population. This challenge constitutes a key part of the backdrop against which future evolution will occur. Genetic engineering technologies are and will continue to be an important component of agriculture; however, we must consider the evolutionary implications of these new technologies. Meeting these demands requires drastic changes in the undergraduate curriculum. Students of biology should be trained in molecular, cellular, organismal, and ecosystem biology, including all living organisms.

Feeding and sheltering people to protect them from famine and disease will be a major challenge for plant biologists, considering the rapid rate of human population growth. According to estimates, the current 6 billion people on earth may increase to as many as 9–10 billion by the middle of the 21st century. Also, current estimates suggest that nearly 800 million people are hungry, and that to meet expanding demands, we need to produce ≈40% more grain by the first quarter of this century. The desire of many countries to develop (and thus use more energy) will put tremendous strain on natural resources and will result in the input of large quantities of greenhouse gases, such as CO_2, N_2O, and CH_4, into the atmosphere. These trends will necessitate a closer association between plant biologists and agricultural scientists concerned with crop production. Thus, because of increasing demands for food and other plant products, research on economically important plants will be intensified in the future. Plant biology has now emerged as a prominent discipline in biology, largely because of progress in understanding the processes of development and gene manipulation at the molecular level (1).

Recent advances in molecular biology of organisms constitute nothing short of a revolution. Our understanding of plant responses and behavior will greatly benefit from the application of molecular biology technologies. The application of molecular techniques has already shown great promise in some important plant products consumed by humans. It is now possible to engineer crops for better yield, make them resistant to diseases and pests, or increase their resistance to drought. For example, genes have been added to rice and maize, two major crops, which allow them to tolerate high levels of aluminum, normally toxic for plants. Furthermore, the development of "Golden Rice" is a major triumph of these new techniques. This rice contains β-carotene, which is converted into vitamin A after the rice is consumed. Thus, people can obtain their required vitamin A by eating rice. Presently there are attempts to use molecular techniques to introduce vaccines into foodstuffs such as bananas, which are consumed in many countries where malnutrition and disease are acute. There is no doubt that various institutions, private and public, will be successful in endeavors such as these in the near future.

Previous Model of Plant Biology

Historically, plant biologists had a simple model for their science. Plant identity (taxonomy), distribution (plant geography), morphology, and physiology were emphasized. With the invention of the microscope, scientists were able to see small processes: internal morphology, development, and the stages in cell division became important subjects for study. Historical plant biology (paleobotany) concerned the evaluation of the progression of vegetation in a given location as the environment changed. It dealt with the relatively slow changes in vegetation in a given region, the evolution of various taxa through geological time, and the evolution of life. Thus, the fields of taxonomy, morphology, and physiology were active. Evolution was approached by assuming the plants were adapted to their environments. With the discoveries of basic principles of inheritance and evolution by natural selection, the science of genetics and evolutionary biology flourished. There was much fascination with convergent evolution, the development of common morphological traits in similar environments across phylogenetically disparate taxa. Many plant biologists sought to accumulate more examples of this interesting phenomenon. Collectively, the investigations of paleobotanists provided a firm foundation for plant biology.

Molecular Biology Revolutionized the Study of Plants

In the second half of the 20th century the discovery of the structure of DNA and RNA, the steps in protein synthesis, and other great discoveries of molecular biology revolutionized the study of plants at all levels, from cells to ecosystems. Taxonomists, evolutionists, ecologists, physiologists, and developmental biologists are now using molecular techniques and are discovering many responses and mechanisms that were not accessible

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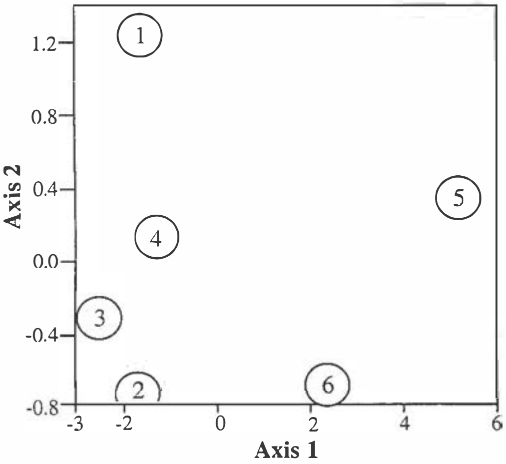


Fig. 1. The influence of spring weather conditions on the development of different communities from a common seed bank in an annual community from the Midwestern United States. Conditions 1–5 represent different weather in the spring.

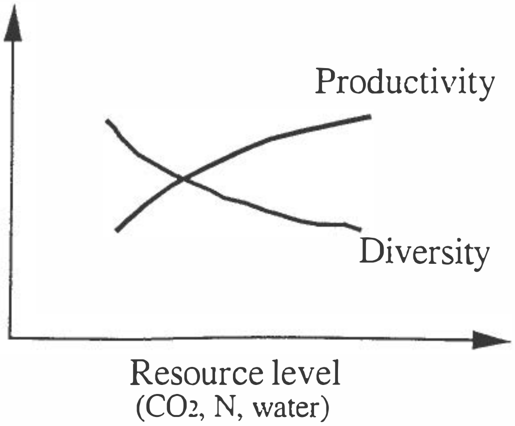


Fig. 2. The anticipated relationship between productivity and species richness in a future climate where variation in weather and resources, e.g., CO_2 and nitrogen, are expected to increase.

in the past. It is now possible to identify, with much precision, the particular genes responsible for traits. And, with the techniques of molecular biology, scientists can introduce or eliminate genes for specific traits. Using these advanced techniques we may also alter the present taxonomy and phylogeny and, as the differences and similarities among taxa are modified by human action, we can create new species.

Remarkably, and despite this great revolution, there will be no significant change in the general structure of plant biology and the relationship between the various branches of the field. These approaches will simply lead to a deeper understanding of the mechanisms and a better control of their direction (i.e., soon we will be able to direct the process, to a certain extent, at will).

Risks of Molecular Biology of Plants

These techniques, however, are not without risks. The resistance to consuming foodstuffs produced by such techniques is a strong indication that, right or wrong, the public at large (particularly in Europe) is not yet ready to totally accept these methods. These techniques, coupled with global change, may create unforeseen problems. For example, the spread of pollen from herbicide-resistant plants to natural populations could be a potential problem. The fear of the spread of resistant varieties to natural populations is warranted, especially for invading plants whose populations are kept low in their native habitats because of diseases and pests. Changes in crop production patterns alone may create unforeseen problems. Under the pressure of increased human demand, planting more corn, as has recently occurred in Ethiopia, may lead to higher population sizes and densities of the larvae of *Aedes aegypti*, which is the vector for transmission of the malaria causal agent *Plasmodium falciparum*. These larvae eat corn pollen that floats on the surface of water bodies. In the meantime, plant populations of native species are being replaced by maize.

The Nature/Nurture Debate in Changing Environments

Because the environment of the future may be quite different from that of today, the nature/nurture argument will become more prominent. All indications suggest that the environment is likely to be more variable than at present. According to many models, temperature and CO_2 levels will rise. Furthermore, it is assumed that night temperature will increase disproportionately (2). Although presently very complicated, the genotype × environment interaction will not simply be ($G \times E$); it will be much more complicated. Instead, $G \times E$ may well be $G \times E_1$, E_2 E_3. . . E_N—depending on the changing environments that the plant experiences through its life cycle and on the speed with which traits travel through the environment. We must remember that E, the environment, has a direct influence on G, the genotype, in turning on and off genes (3). Also, we do not know which subset of G or E will impact the most strategies of variation and fitness. All expectations suggest that the role of environmental variation may be increased. Broad-niched species apparently respond well to global change, and it has been suggested that they will be impacted less than narrow-niched species (4). Thus it is expected that as increased environmental variation tends to eliminate narrow-niched (specialized) species, broad-niched species or species that are inherently genetically variable and/or plastic in their response to environmental change will be favored (5). The elimination of these species may also lead to a reduction in biological diversity, presently a major concern for humanity (6). By their nature, broad-niched species (which are usually early successional) can tolerate a wider range of environmental variability than narrow-niched, more stable, late successional communities (see ref. 4). In this case, there may be strong selection for plasticity in plants (7) or for broad-niched genotypes and early successional species (as discussed earlier). Because it is fast growing, the potential increased abundance of early successional species may have significant implications for global carbon sequestration. On the other hand, environmental variation can lead to the divergence of communities with different dominant species, thus increasing between patch diversity (B diversity). An illustration of this situation is the development of different communities from similar seed banks when they are exposed to a range of spring conditions e.g., wet, dry, cold, warm, etc. (Fig. 1). These results seem to support the "Initial Condition" hypothesis of the proponents of complexity theory. Furthermore, in a future environment with additional resources, such as nitrogen due to deposition, there is the possibility of an increase in productivity and a decrease in diversity (Fig. 2). This result may occur for two reasons: (*i*) species in the same ecosystem do not respond in the same manner to elevated atmospheric CO_2, thus CO_2-responsive species may become dominant and exclude other less-responsive species, and (*ii*) they do not respond similarly to nitrogen deposition.

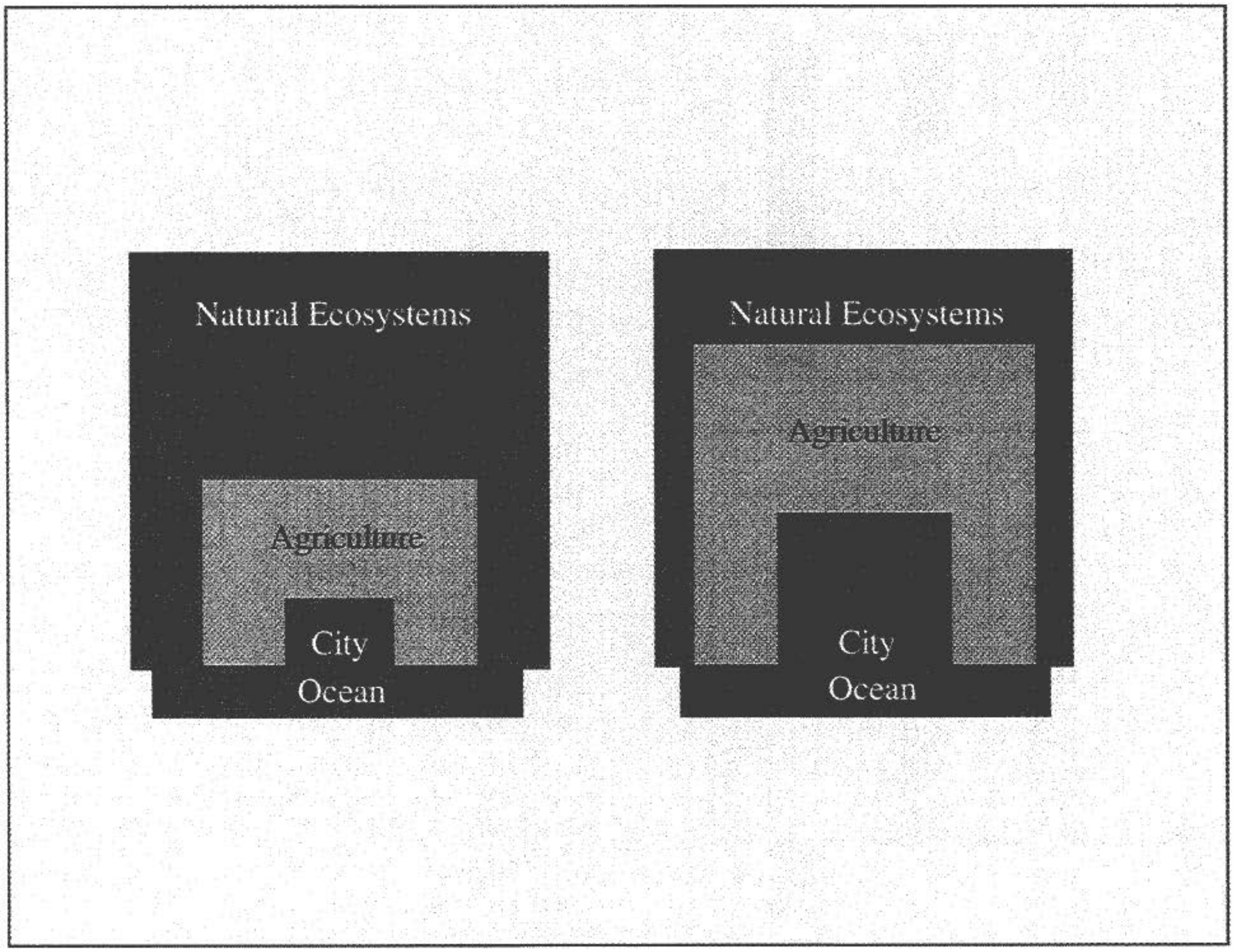


Fig. 3. Diagram showing the change in the area of natural vegetation in the future, where the number of people on earth approaches 10 billion.

Economic Plants and Environmental Variability

In a rapidly changing environment with an ever-increasing human population, work on plants of economic value will have to be intensified. We need to produce varieties with a broader response to the varying environment. The separation between agricultural science and basic plant biology will become less clear as more and more plant biologists work on economically important species and perhaps find (or design) new ones. Thus, the following should be among the aims of plant biologists of the future:

(*i*) To engineer crops that can resist drought and other resource limitations, such as soil nutrients, enabling people to cultivate marginal, presently unproductive, land more successfully;

(*ii*) To increase yield by bioengineering and classical hybridization techniques of major crops; and

(*iii*) To enhance nutritional quality without sacrificing quantity.

Increasing yield usually requires an increase in the application of fertilizer and biocides. This means that we have to manufacture more fertilizers and biocides, and both processes need energy. In fact, the quantities of manufactured nitrogen fertilizer already exceed the amount of nitrogen fixed naturally (8). We do not know the impact of the high-nitrogen production levels on the environment, although we suspect it has negative consequences. Without an increase in the application of fertilizers, something that the developing countries presently cannot manufacture or purchase, it would be difficult to achieve an increase in crop production and maintain quality. Agricultural runoff and pollution by nitrogen and phosphorous fertilizers are major problems, which already are having a detrimental impact on biological drinking water and diversity in parts of the world. Land disturbance may cause large quantities of dust to be added to the atmosphere, compounding the environmental pollution problem (9), but may increase the impact of newly needed nutrients on the soil.

There is no escape from the fact that, with the increase in human populations, the area of natural ecosystems remaining will be reduced, as more land is going to be used to support the billions of people (Fig. 3). However, the area for agriculture relative to population size will likely decrease because of improvements in productivity brought about by molecular biology. A subject of major concern will be the simplification of natural and agricultural systems and a reduction in global biological diversity. These systems can be modified to the point that they cannot supply the necessary services for humanity. It has been suggested (10) that the differences in productivity between developed and developing countries will be magnified as models predict an increase in crop production in the developed countries and a decrease in developing countries (Fig. 4). This situation can have major political and social implications and requires immediate attention.

One last point: the quality of agricultural products may become a big problem in the future and may require extensive work in agricultural molecular biology. Elevated CO_2 may influence the C/N ratio and possibly protein content, reducing

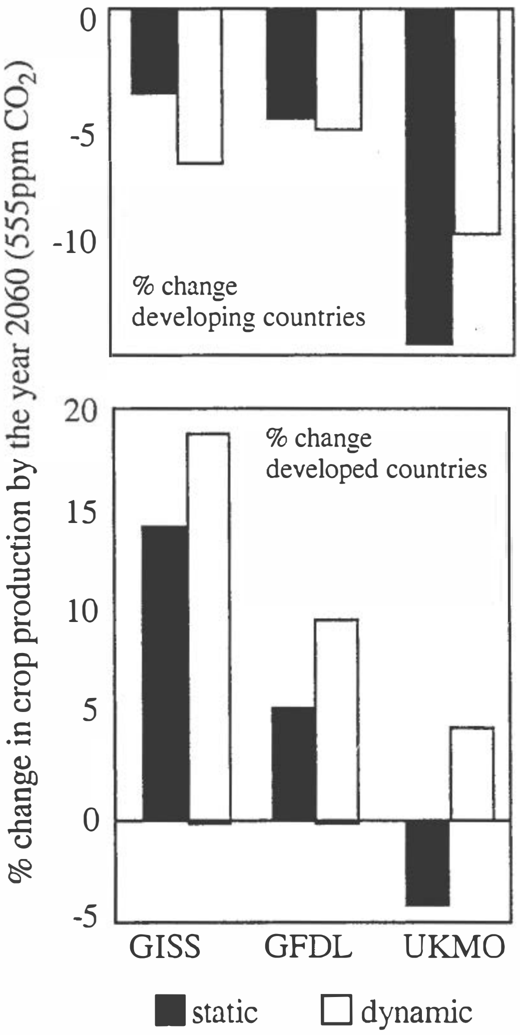
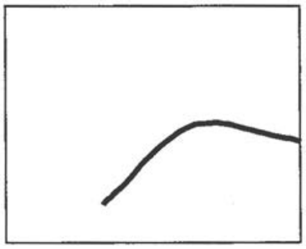


Fig. 4. Three model predictions of changes in grain yield in developed (increase) and developing (decrease) countries (from ref. 9).

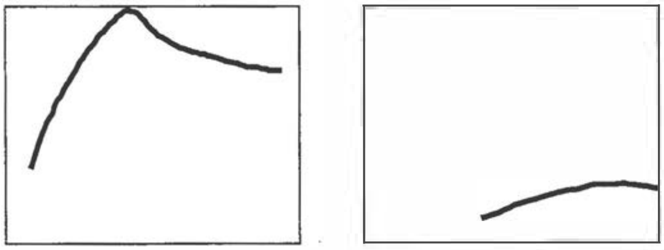
the nutritional quality of crops. For example, when we grew wheat in ambient and high CO_2, the resulting grain from the elevated CO_2 yield was not suitable for bread-making according to U.S. Department of Agriculture mixogram analysis. [A mixogram tests the protein strength in the grain and estimates mixing tolerance and ability to produce quality bread (Fig. 5).]

A Curriculum to Train Plant Biologists for the Future

Advances in plant biology through the use of the techniques of molecular biology and other approaches and the expected integration of various levels of inquiry in the field dictate that a new curriculum of study be espoused. Of course, there are many possibilities. Plant biologists should be aware of these advances regardless of the level of organization at which they work. For example, in addition to a course in integrative biology presenting the principles of biology to all college biology students, these students should have good grounding in molecular, cell, organismic, and ecosystem biology. The first two fields, molecular and cell biology, should not be presented, as they are now in many universities, with the exclusion of plants, bacteria, protists, fungi, and archaea. Molecular biology courses of the future should address animals, plants, bacteria, and all other taxa, and the similarities and differences among these organisms should be made clear. Then students can take from a variety of courses those that are related to their area of study and specialization. For example, cell-wall structure and biosynthesis and the details of the biophysics and biochemistry of photosynthesis (plant characters) should not be ignored in courses on cell biology. In fact, we may wish to examine the usefulness of a 4-year college or a 5- to 6-year Ph.D. program to fulfill these requirements, to see whether these periods are long enough to accommodate the new biology. Another option is to drop some subjects that appear unnecessary or have already been covered in high school. Enacting changes in the curriculum will require clear thinking and a daring attitude.



Original wheat seed ·



Ambient CO_2 / High nitrogen
(Current conditions in
developing countries)

High CO_2 / High nitrogen
(Future conditions)

Fig. 5. Mixogram (produced by the U.S. Department of Agriculture) of wheat grown from the original seed at ambient and high CO_2 and fertilized with nitrogen. (Based on L. T. Meyer and F.A.B., unpublished data.)

Conclusions

(*i*) The techniques of molecular biology are revolutionizing the study of plants and will be used more and more by all plant biologists to discover the mechanisms of development and the control of developmental processes.

(*ii*) Disease- and herbivore-resistant plant varieties will be developed by agricultural scientists and applied botanists. This may lead to the development of new taxa and phylogenies.

(*iii*) To feed the burgeoning human population, the gap between applied and theoretical plant biology should narrow. More work will be done by plant biologists on economically important plants.

(*iv*) The science of ecology will become more important as the issues that face humanity become more ecological in nature.

(*v*) The basic structure of plant biology may not change. Great interest will remain in phylogeny, genetics, development, physiology, morphology, and ecology.

(*vi*) A new curriculum is needed in biology that emphasizes the unity of biology. Plant biology students should have a basic understanding of molecular, cell, and organismic biology and ecosystem ecology.

Attempts to correctly predict the future will depend on good data and good models. We should not shy away from the approaches of molecular biology. We should be prepared to accept mistakes, as these will undoubtedly occur.

1. Kende, H. E. (2000) *Science* **287,** 591 (lett.).
2. Intergovernmental Panel on Climate Change (IPCC) (1995) *Climate Change 1995: Impacts, Adaptations and Mitigation of Climate Change; Scientific-Technical Analyses*, eds. Watson, R. T., Zinyowera, M. C., Moss, R. H. & Dokken, D. J. (IPCC, Cambridge Univ. Press, Cambridge, U.K.)
3. Bazzaz, F. A. & Stinson, K. A. (1999) in *Physiological Plant Ecology*, eds. Scholes, J. D. & Barker, M. G. (British Ecological Society, London), pp. 283–295.
4. Bazzaz, F. A. (1996) *Plants in Changing Environments: Linking Physiological, Population, and Community Ecology* (Cambridge Univ. Press, Cambridge, U.K.).
5. Miao, S. & Bazzaz, F. A. (1990) *Ecology* **71,** 2166–2178.
6. Wilson, E. O. (2000) *Science* **289,** 2279.
7. Ackerly, D. D., Dudley, S. A., Sultan, S. E., Schmitt, J., Coleman, J. S., Linder, C. R., Sandquist, D. R., Geber, M. A., Evans, A. S. & Dawson, T. E. (2000) *BioScience* **50,** 979–995.
8. Vitousek, P. M. (1994) *Ecology* **75,** 1861–1876.
9. Chadwick, O. A., Derry, L. D., Vitousek, P. M., Hubert, B. J. & Hedim, L. O. (1999) *Nature (London)* **397,** 491–497.
10. Fischer, G., Frohberg, K., Parry, M. L. & Rosenzweig, C. (1996) in *Global Climate Change and Agricultural Production*, eds. Bazzaz, F. A. & Sombroek, W. (Wiley, West Sussex, U.K.), pp. 199–235.

Colloquium

The evolutionary impact of invasive species

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Since the Age of Exploration began, there has been a drastic breaching of biogeographic barriers that previously had isolated the continental biotas for millions of years. We explore the nature of these recent biotic exchanges and their consequences on evolutionary processes. The direct evidence of evolutionary consequences of the biotic rearrangements is of variable quality, but the results of trajectories are becoming clear as the number of studies increases. There are examples of invasive species altering the evolutionary pathway of native species by competitive exclusion, niche displacement, hybridization, introgression, predation, and ultimately extinction. Invaders themselves evolve in response to their interactions with natives, as well as in response to the new abiotic environment. Flexibility in behavior, and mutualistic interactions, can aid in the success of invaders in their new environment.

The Nature of the Problem. Those of us alive today are witnessing the consequences a number of truly grand, but unplanned, biological experiments. They are the result of the activities of a massive human population that is still growing and increasing its impact on the Earth. Because there are no controls on these experiments, as such, we must look to biological patterns through time for perspective on the consequences of the mixing of biotas. This is a challenge because environments of the past also changed, sometimes abruptly.

These historical fluctuations in climate and biota of the past have led some to say that nothing new is happening that has not already happened before. The response to this proposition is yes, but the *rate of change* in the composition of the atmosphere today exceeds anything of the past, as will the consequent rate of climate change. This is also true to a large degree in the extent of migration of species among continents. Before the Age of Exploration, dispersal of organisms across these great biogeographic barriers was a low-probability event; however, today this is routine. In this paper we briefly summarize the consequences of the massive movement of organisms across these barriers in terms of the course of future evolution.

We start this essay with two quotes providing perspectives on the problem. One is from the pioneering work of Charles Elton (1), who stated, "We must make no mistake: we are seeing one of the great historical convulsions in the world's fauna and flora." Elton certainly had no doubts of the magnitude of the invasive species issue. More recently, Geerat Vermeij (2) remarked specifically about the evolutionary consequences of this convulsion, ". . . if newcomers arrive from far away as the result of large-scale alterations in geography or climate, the change in selective regime and the evolutionary responses to this change could be dramatic." We examine here some of the evidence for this potentially dramatic scenario.

The Changing Evolutionary Landscape. It is commonly acknowledged that the abiotic environment is being greatly altered because of massive land-use alteration and emerging climate change (3, 4). However, an equally drastic alteration is occurring in the composition of biotic communities. The kinds of physical and biotic environments that exist now are quite different from those that have existed in recent geological times.

International commerce has facilitated the movement of species; this is true globally and across taxonomic groups. Ironically, this has increased species richness in many places where new species are introduced. The actual numbers of individuals and species being transported across biogeographical barriers every day is presumably enormous. However, only a small fraction of those transported species become established, and of these generally only about 1% become pests (5). Over time however, these additions have become substantial. There are now as many alien established plant species in New Zealand as there are native species. Many countries have 20% or more alien species in their floras (6). There are few geographic generalities to these trends; the strongest is that islands, in particular, have been the recipients of the largest proportional numbers of invaders. Biotic homogenization within continents is equally as striking as mixing among oceans. As one example, Rahel (7) notes that in the United States pairs of states on average now share 15 more species than they did before European settlement. The states of Arizona and Montana, which previously had no fish species in common, now share 33 species in their faunas.

Mack (8) estimates that over the last 500 years, invasive species have come to dominate 3% of the Earth's ice-free surface. Vast land or waterscapes, in certain regions, are completely dominated by alien species, such as the star thistle *Centaurea solstitialis* in the rangelands of California, cheatgrass (*Bromus tectorum*) in the intermountain regions of the western United States, and water hyacinth (*Eichornia crassipes*) in many tropical lakes and rivers.

The Rates of Exchange. As the volume of global trade increases, one would expect the rate of establishment of alien species to increase also; data support this prediction. Cohen and Carlton (9) noted that the rate of invasion into San Francisco Bay has increased from approximately one new invader per year in the period of 1851–1960, to more than three new invaders per year in the period of 1961–1995. In the United States the numbers of fish introductions, either from foreign sources or across watershed boundaries, has increased dramatically. In the period between 1850 and 1900, 67 species were introduced, between 1901 and 1950, 140 species, and between 1951 and 1996, 488 species (ref. 10 and the web site referred to therein).

In addition to the greater number of species crossing borders there is also a buildup in the invasive potential of those nonnative species already established in a region, as immigration increases their population sizes. "Introduced species" may stay at a fairly low population size for years and then explode at some later date—the so-called lag effect. This lag effect may simply be the result of the normal increase in size and distribution of a population. For instance, *Bromus tectorum* was introduced to

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intermountain western North America around 1890, and remained in localized populations for 20 years. This lag phase was followed by 20 years of logistic range expansion; by 1930 *B. tectorum* was dominant over 200,000 km^2 (11).

Crooks and Soule (12) note that in addition to the normal population growth lag phase there are other mechanisms that can keep newly introduced species at low levels for decades before they become invasive. These include environmental change, both biotic and abiotic, after establishment and genetic changes to the founder populations that enable subsequent spread. Evidence for the former cases is abundant but scarce for the latter.

In summary, the biotic background for evolution has been changing since the Age of Exploration, and at an ever-accelerating pace because of accumulative effects of the numbers of species involved, the increased rate of exchange, and the lag debts that communities have amassed.

Looking to the Past. There are examples from the past of sudden mixing of biotas that were formerly isolated; one of these is fairly recent and instructive. The biota from the Red Sea and the Mediterranean Sea were reconnected, after a separation of millions of years, by the construction of the Suez Canal in 1869. The pathway for movement between these water bodies has changed since 1869 because of the varying salinity of a lake in the canal system; that is, there has not been totally free exchange without barriers. Nonetheless, over 250 species, 34 new genera, and 13 new families have moved into the Mediterranean Sea from the Red Sea, yet there has only been one documented extinction (13). These invasions have primarily been accommodated by niche displacements through competitive interactions among the congeners (14). Many of the native fish in the Mediterranean have maintained their preinvasion feeding habits but have been displaced in depth by the Red Sea invaders, which prefer the shallower, warmer, waters at the surface (15). Two nocturnally foraging fish (*Sargocentron rubrum* and *Pmpheris vanicolensis*) have shown large population increases after invading the Mediterranean from the Red Sea. Night foraging is an uncommon strategy among native Mediterranean fish (only one feeds at night), hence these migrants were probably successful because this novel behavior allowed them to exploit resources that the native fauna had not yet used.

There have been a number of spectacular population explosions of the Red Sea immigrants through time, most of which have eventually become reduced in size (14). An exception is *Rhopilema nomadica*, a large Red Sea jellyfish that experiences population explosions and crashes each summer off the coast of Israel.

The Great American Interchange of biota, the result of the isthmian land bridge that formed during the Late Pliocene, provides further information on the consequences of the mixing of previously isolated biota. However, the course of temporal resolution of the information available does not make it possible to say with certainty whether the losses of biota that occurred subsequent to the bridge were due to competition with new arrivals, although it appears likely (16). The effects of the interchange apparently were asymmetrical, with the immigrants from the south "insinuating" into the northern biota, whereas the northern immigrants to the south may have caused extinctions and undergone subsequent evolutionary radiation (17).

What we lack is detailed information on the impacts of the exchanges of biota on time frames greater than centuries but less than millions of years. In the century time frames we have processes that are still in a state of flux at the community level and ones that have been that have not been studied in detail. In the geological time frame, the poor temporal resolution does not permit us to clearly understand the mechanisms that have led to what we see in the fossil record.

The Direct Evolutionary Consequences of Mixing

Evolutionary Adjustments of Invaders and of the Invaded. We turn to contemporary studies to give us some indication of the evolutionary impact of invasive species. Recent studies have shown that invaders can rapidly adapt to the new environments in which they find themselves. Huey *et al.* (18) demonstrated how an introduction of a new fruit fly into the west coast of North America resulted in the evolution, in only 20 years, of an apparently adaptive cline related to wing size, throughout the vast new latitudinal range extending from southern California to British Columbia. The cline that developed in North American female flies was similar to that found in the European native populations. Interestingly, the developmental basis for the cline of wing size was different in Europe than for the invader in North America, although the functional result was the same, providing additional evidence for the adaptive advantage of this set of traits.

Drosphilia subobscura were introduced into North America in 1982; shortly thereafter Ayala *et al.* (19) described the invasion as "a grand experiment in evolution." This was certainly an accurate prediction, given the results of Huey *et al.* 10 years later, and only 20 years after the beginning of the invasion event.

There are other documented instances of an invading species adapting to its new environment. For example, Johnston and Selander (20) described the evolution of apparently adaptive clines in body size and feather color in English sparrows that were introduced into North America in 1852 and that subsequently established a large geographical range. Further, Cody and Overton (21) described the reduction in distance of dispersability for wind-dispersed seeds of invasive species onto islands in just a few generations in small isolated populations. Similarly, Losos *et al.* (22) demonstrated that within 10–14 years species of lizards introduced onto a series of island in the Caribbean showed adaptive morphological adjustments.

There are also examples of relatively rapid, nonadaptive, genetic change of invaders as seen in house mice introduced into Madeira; localized differentiation of chromosomal races is the result of genetic drift in isolated valleys (23). Similarly, genetic drift has been responsible for geographic genetic patterns found in the introduced *Bufo marinus* in Australia (24).

Evolution in Response to an Invader. There are also examples of rapid evolution in native species in response to an introduced species. Carrol and Dingle (25) indicate that populations of the soapberry bug (*Jadera hematoloma*) have evolved differing beak lengths in response to the introduction of new invasive hosts, within only 50 years time. Singer *et al.* (26) have shown rapid evolution in the feeding preferences of the *Euphydras* butterfly for the invading herb, *Plantago lanceolata.*

Zimmerman (27) documents an interesting case of evolution in response to an introduced crop species. At least five species of host-specific moths (*Hedylepta*) have evolved since the introduction of banana into Hawaii ≈1,000 years ago. These species were threatened at the time of Zimmerman's study by parasitic wasps and flies introduced for agricultural pest control.

There is a large literature on the evolution of weeds in response to human activities, including agricultural practices. Harlan (28) noted that some weeds have evolved to be crop mimics. Not only are they are similar in their phenological development and morphological appearance to the crops with which they have co-evolved, but also their seeds have evolved a similar appearance so they are not sorted and discarded during harvesting. For example, the lentil mimic (*Vicia sativa*) has evolved a seed shape and color comparable to the lentil (*Lens culinaris*). This trait is under control of a single gene. Similarly, *Echinochloa crus-galli* has evolved mimics to rice, *Oryza sativa*, which are very difficult to distinguish from the crop.

De Wet and Harlan (29) surmised that many plant weeds might have evolved from natural pioneer species associated with continuous disturbance by humans. Some weeds that have developed in association with agriculture have become crop mimics as described above. Weeds are also derived from hybridization and introgression with crops as happened with Johnson grass (*Sorghum halepense*) and the cultivated *Sorghum bicolor*. Weeds have also evolved from abandoned domesticated plants.

Thus there are many cases that have been documented of the evolutionary response to the new environment that an invasive species may encounter as well as cases of the adaptive response of organisms to a new invader.

Hybridization and Introgression. In addition to direct evolutionary responses of organisms involved in invasions there are also very important indirect effects through changes in the genetic structure of invasive species in relation to the new organisms that they encounter. These major effects are related to hybridization and introgression. Rhymer and Simberloff (30) have recently summarized our knowledge in this area. There are many examples extending over many different taxonomic groups, a few of which are noted below. These authors conclude that in the case of invasive species hybridization with native species can cause a loss in fitness in the latter and even a threat of extinction. McMillan and Wilcove (31) have documented that of 3 of 24 species listed as Endangered in the United States and that subsequently went extinct, 3 were the result of hybridization with alien species.

Birds—Mallard ducks (*Anas platyrhynchos*) that have been introduced into various regions of the world have had large genetic effects. They have hybridized and reduced populations of the New Zealand gray duck (*Anas superciliosa superciliosa*), the Hawaiian duck (*Anas wyvilliana*), and the Florida mottled duck (*Anas fulvigula fulvigula*) (30).

Mammals—Sitka deer (*Cervus nippon*) were introduced into Great Britain from Japan over a hundred years ago. They have hybridized with the native reed deer (*Cervus elephaus*) although they are different in body size. It appears that the genetic integrity of the native red deer is threatened in some regions (32).

Fish—There are a number of cases of hybridization and subsequent introgression in fish, primarily game fish where there are massive introductions of foreign stock. These include trout in western and eastern United States as well as in Europe (33, 34). It has been shown, however, that even small introductions of nonnative species can have large impacts on the genetics of native species through hybridization and introgression, as was found for native pupfish in Texas (33).

Plants—Abbott (35) notes that of 2,834 species listed in the New Flora of the British Isles 1,264 are aliens. There are 70 recognized hybrids between native and alien species and 21 between aliens. About half of these hybrids show some degree of fertility.

There are many examples of the large populations of invading species swamping small populations of native species by hybridization, but in certain cases small populations of an invader can threaten native species that have much larger populations. This is the case with the invading *Spartina alterniflora* into the San Francisco Bay. It hybridizes with the native *Spartina foliosa.* The invader has a higher pollen output, and greater male fitness, than the native species and the hybrids and it occupy lower intertidal habitats. In time introgression will threaten the native species (36). Conversely, small populations of rare species can be threatened by hybridization in a number of ways (37), including infertility of the hybrids.

Small populations on islands are particularly vulnerable to extinction by hybridization because they are often less genetically divergent than mainland species and have weak crossing barriers as well as unspecialized pollinators. Levin *et al.* (37) describe a number of cases of extinction by hybridization on islands, including the endemic shrub *Cercocarpus traskaei* with the widespread *Cercocarpus betuloides* and the endangered *Lotus scoparius traskiae* with the *Lotus argophyllus ornithopus*. They specifically note that introductions may threaten rare species on islands and give a number of examples from around the world, including threats to the rare *Arbutus canariensis* and *Senecio teneriffae* on the Canary Islands, *Gossypium tomentosum* on the Hawaiian Islands, and *Pinguicula vulgaris* and *Linaria vulgaris* in the British Islands. They posit that the threat of extinction of rare species by hybridization is very high and that habitat disruption and invasive species are increasing this threat to the degree that conservation programs should strive to isolate rare species from cross-compatible congeners.

The Origin of New Taxa Through Hybridization and Introgression. While hybridization with invaders can be a threat to species integrity, it can also be a source of new variation and the origin of new species. *Spartina alterniflora* from the east coast of North America was introduced into Southampton in shipping ballast in the early 19th Century. It subsequently hybridized with the local *Spartina maritima,* producing a sterile hybrid. The hybrid in turn underwent chromosome doubling to produce the new fertile species, *Spartina anglica. Spartina anglica* has become very aggressive and occupies large areas of the coastline of the British Isles while at the same time the original invader, *Spartina alterniflora*, and the native *Spartina maritima* have maintained limited distributions. The new polyploid evidently has characteristics that enable it to occupy bare tidal flats that were not available to the parents (38). This event was apparently serendipitous and has not been replicated artificially (39).

In addition to the *Spartina anglica* there are other cases of alloploids that have originated from hybridization of native and invasive species. These include species of *Tragopogon* in North America and *Senecio* in Great Britain (35).

There are also examples of introgressive hybrids between native and weedy species becoming stabilized to form new taxa. The introduced *Helianthus annuus* hybridized with native *Helianthus debilia.* The hybrids adapted to the new conditions it encountered to form the subspecies *Helianthus annuus texanus.* Abbott (35) cites six such cases of origins of new taxa.

The Indirect Evolutionary Consequences of Mixing

Behavioral and Trait Shifts. In addition to the evolution of traits to adapt to new environments and to new invaders there are cases of behavioral shifts in the invaders themselves or in response to invaders. Holway and Suarez (40) give examples of shifts in behavior of populations of invading species from that found in their native ranges. Two ant species originating from Argentina (the fire ant *Solenopsis invicta* and the Argentine ant *Linepirtma humile*) both exhibit these shifts. It is not known whether these shifts are founder effects or adaptive. These authors make the case that behavior should be more fully incorporated into research as we build an understanding of the invasion process.

The introduction of brown trout into the streams of New Zealand started in the mid-1800s. They have driven to extinction some local populations of native fish and, in addition, they have evidently resulted in changed behavior of native mayfly nymphs and, to a certain extent, crayfish (41).

In addition to behavioral shifts, either in response to an invader or in response to the new biotic community that an invader encounters, shifts in traits have been observed in an invader in a new environment. Blossey and Notzold (42) note that in populations of invasive species, the individuals are often larger in their new territory than in their native land. They compared plants from populations from the United States and as well as those from Europe where they are subject to natural predation in their native habitat. They attributed the size differences to the consequences of natural selection for greater competitive capacity after release from herbivore attack and the need to produce defensive compounds. Although this particular explanation has been challenged (43), others have noted similar cases of this phenomenon in comparing invading plants from Australia into California (44) and comparing invasions from South Africa into Australia and *vice versa* (45).

Invasive ants may also benefit from release from native pathogen populations, leading to larger colony size that confers greater exploitative competitive capacity, as discussed in Holway (46) and Human and Gordon (47) (see below). Colonies of invasive Argentine ants are larger in areas where they invade than they are in their native habitat.

Niche Displacement. Gray squirrels (*Sciurus carolinensis*) from North America have displaced the native red squirrel (*Sciurus vulgaris*) throughout most of the deciduous and mixed woodlands of Britain. This displacement apparently has resulted from food competition between these species, with gray squirrels favored by high quantities of oaks in the canopy. Recent decline of hazelnuts over oaks has evidently contributed to the demise of the red squirrel (48).

There has been a detailed study of the interaction between a California native mudsnail, *Cerithidea californica,* and an invasive mudsnail, *Ilyanassa obsoleta*, from the American Atlantic. Populations of *Ilyanassa* have locally displaced *Cerithidea* from the open tidal flats, restricting its distribution to the upper intertidal area. *Cerithidea*'s former functional role has been taken over by *Ilyanassa* (49).

Douglas *et al.* (50) have described the apparent niche shift in the native fish *Meda fulgida* when they co-occur with the introduced red shiner (*Cyprinella lutrensis*).

Competitive Exclusion. Some invasive species completely eliminate native species through competitive exclusion. The invasive fire ant (*Solenopsis invicta*), for example, has had a devastating effect on the arthropod biota that it encounters. In a detailed study in Texas, it was found that this fire ant reduced native ant diversity by 70% and the total number of native ant individuals by 90%, apparently by competitive exclusion. Similarly, overall non-ant arthropod diversity was reduced by 30% and the numbers of individuals by 70% (51). It should be noted, however, that while the fire ants excluded some native species from the invaded areas, the natives persisted in nearby uninvaded areas, such that no extinctions were observed.

The Argentine ant (*Linepithema humile*) is a widely distributed invasive species that displaces native ants throughout its introduced range. It does so by being a better competitor for food resources than the native species (46, 47).

There are accumulating studies examining the mechanisms of competitive displacement of native species by invaders. As examples, superior competition for food resources has resulted in the replacement of the native gecko, *Lepidodactylus lugubris*, by the invading *Hemidactylus frenatus*, throughout the Pacific (52). A higher resource-use efficiency of the available food resources has been implicated in the competitive superiority of the introduced snail *Batillaria attramentaria* over the native mud snail *Cerithidea californica* in the salt marshes and mud flats of northern California (53). Studies have also shown that behavioral differences in aggression and predation between a native and an invading amphipod explain competitive displacement (54). Competition for space by the invading mussel *Mytilus galloprovincialis* from southern Europe has displaced native mussels in California and South Africa (55).

Studies of such new interactions, brought about by invaders, are particularly revealing on the nature of competition because in "stable" ecosystems, with a long history of competition among its members, the resulting evolution of niche displacement makes it more difficult to observe the direct competitive process.

Mutualisms. In any ecosystem there is a web of interaction among the biotic components of differing specificities. Mutualisms, the tightest of such interactions, would seem to be a barrier to the success of a single player of a partnership becoming an invasive species. There is some evidence for this in the fact that nonmycorrhizal (i.e., do not depend on mutualistic root fungi) plant taxa, such as the Brassicaceae and the Chenopodiaceae, are particularly successful weeds. However, quite often the tightness of mutualisms is not as great as supposed and other species in the new habitat can play the required role for the invader (e.g., pollination). There are also examples of the arrival of one nonnative species, and the subsequent arrival of a co-evolved facilitator, thereby increasing the success of each in its new environment. This has happened with *Pinus* spp. and their mutualistic mycorrhizal fungi in the Southern Hemisphere; Richardson *et al.* (56) describe these as well as other examples.

With the mixing of biota and thus new interaction potentials there is the great possibility of new kinds of mutualistic relationships evolving. Richardson *et al.* (56) note several such cases, including the dispersal of North American and European pine seeds, which are normally wind-dispersed, being dispersed into new areas by cockatoos and European pines being dispersed in South Africa by alien American squirrels. Simberloff and Von Holle (57) also note cases of one invading species facilitating the success of another, including a bird of Asian origin being the prime disperser of a shrub from the Canary Islands, all in their new Hawaiian home.

There are also instances of an invasive species disrupting mutualistic relationships (58). Native seed-harvesting ants disperse the seeds of certain proteas in South Africa. These native ants have been displaced by Argentine ants that are not successful in dispersing the *Protea* seeds to suitable germination microsites, thus potentially leading to the extinction of rare and endemic *Protea* species.

Finally, there are striking examples of host shifts as species are mixed through invasions and a parasite of one infects the other which is less able to cope with the parasite, as is happening with the parasitic mite *Varroa jacobsoni,* which evolved as a brood parasite of the Asian hive bee, *Apis cerana*, but which has now also switched host to the western honeybee, *Apis mellifera*, with disastrous results (59).

Extinctions. Invasive species not only alter competitive interactions and reduce native populations within a community but they can also lead to extinctions. Overall they are considered the second greatest threat to imperiled species in the United States (60). Carlton *et al.* (55) make the useful distinction among extinction events as local, regional, or global extinctions. They also recognize functional extinctions where individuals of a species are so reduced in numbers that they no longer play a major role in ecosystem processes. Thus there is a large continuum of impacts, with the main concern and statistical information available on the total global extinction of a species whereas, of course, local extinctions and population reductions are important in ecosystem functional considerations as noted by Carlton *et al.*

The literature abounds with examples of invasive species driving local native species to extinction, primarily on islands, and especially involving predators. Rodda *et al.* (61) detail the particularly dramatic case of the impact of the invasive brown tree snake (*Boiga irregularis*) on the biota of Guam, which has caused a major conservation crisis through negative effects on birds, reptiles, and mammals. In a review of the impacts of introduced species on reptiles on islands Case and Bolger (62) note that, "Although competition has led to changes in abundance and has caused habitat displacement and reduced colonization success, extinctions of established reptile populations usually occur only as a result of predation." They do note the large number of examples of the latter that have occurred as a result of predation by rats, feral cats, and mongooses.

It has been well documented that of all ecosystems lakes and streams have been most modified by invasive species, mainly because of the persistent efforts of humans to stock with game fish. Many of the introductions into these bodies result in species enrichment rather than extirpation (63). However, one of the most spectacular example of species extinctions in lakes comes from the introduction of the Nile perch into Lake Victoria, resulting in the loss of hundreds of species of cichlid fish (64). Ricciardi and Rasmussen (65) call attention to the fact that the freshwater fauna of temperate North America has extinction rates matching that of tropical forests, in part because of invasive species. Ricciardi *et al.* (66), for example, note a global pattern, that within 4–8 years after invasion by zebra mussel (*Dreissena polymorpha*) local native mussel populations are extirpated. Over 60 endemic mussel species of the Mississippi River Basin are threatened with global extinction by the effects of zebra mussel and environmental degradation.

Although the introduction of an organism into a new environment always provides risks and surprises as to the impact it will have on other organisms, it is particularly disconcerting when organisms that are introduced to control the activities of an unwanted invader instead do collateral damage to other species, even driving them to extinction. This is apparently the case with the introduction of the rosy wolf snail, *Euglandina rosea*, which was imported into Hawaii in 1958 to control the giant African snail, *Achatina fulica*. Unfortunately, *Euglandina* did not restrict its predatory activity to the African snail but also attacked rare native Hawaiian snails (67), apparently driving some to extinction. Between 1977 and 1987 *E. rosea* pushed the endemic tree snails of the island of Moorea to extinction (68). There is another extinction crisis in the making with the movement of *Cactoblastis cactorum* from its point of introduction for the control of *Opuntia* in the Caribbean, to a trajectory that will bring it to a center of diversity of *Opuntia* in Mexico (H. G. Zimmermann, personal communication).

There have been attempts to give us some sense of the ultimate result of the mixing of the biota of world. Brown (69) has calculated, based on species–area relationships, the worst-case scenario for the impact of free exchange of biotic material across former biogeographic barriers. This was done assuming the Earth's land surface was contained into one supercontinent but that the current climates and geological features were maintained. With these assumptions there would be massive decrease in species, amounting to 65.7% for land mammals, 47.6% for land birds, 35% for butterflies, and 70.5% for angiosperms. McKinney (70) has made similar calculations for the ocean and concludes that there would be a reduction of about 58% in the current diversity. McKinney points out, however, that for the theory to be fulfilled there would have to be unfiltered faunal exchange around the world and the lack of physical variability. McKinney notes that it is because these conditions are not fulfilled that we have not seen extinctions in relation to the Suez Canal exchanges.

Concluding Remarks

In the course of this review we have discussed the mechanisms by which invasive species evolve in response to their new biotic and abiotic environments, and how invasive species have altered the evolutionary trajectory of native species with which they interact. While it is not surprising that an invasive species would evolve in their new habitat in response to a new set of selective pressures, it is surprising that there are a number of clear examples of evolutionary shifts in native species in response to the presence of invaders, given the small number of generations involved in interactions, and the short period for which such interactions have been studied by ecologists and evolutionary biologists. Much of the evidence we have reviewed has been observed in islands, reinforcing what we know of islands as evolutionary hotspots. While few generalizations can be made across taxa and across environments, we can venture a few tentative conclusions. First, invasive predators may have the most dramatic effects, as the extinctions they cause represent an irreversible removal of evolutionary potential. Second, few examples of extinction have been associated with competitive interactions. This indicates either that extinction by competition is a slower process than extinction by predation, such that the end product of the process is not likely to be observed on the time scale of most scientific studies, or that communities are not as "full" as most ecological theories presume. Third, interactions between invasive and native biota demonstrate how global changes that alter community structure can have persistent and unexpected consequences.

The biota of the Earth is undergoing a dramatic transformation. The spatial patterning, structure, and functioning of most of the ecosystems of the world have been altered by the activities of humankind. There is every indication that these trends will intensify as the size of the human population continues to grow, even in systems that have been set aside for protection, because of the global changes that have been set in motion that are affecting the atmosphere and the climate. Although some aspects of global change, such as climate change, may be reversed by societal actions, this will not be possible for biotic exchange. The mixing of formerly separated biota, and the extinctions these introductions may cause, are essentially irreversible. Since the beginnings of the Age of Exploration, humans have purposefully and inadvertently moved biological material across barriers that, for recent evolutionary time, have separated the unique biotic realms of the continental land masses. We are now developing a whole new cosmopolitan assemblage of organisms across the surface of the Earth with large consequences not only for the functioning of ecosystems but also for the future evolutionary trajectory of life.

1. Elton, C. S. (1958) *The Ecology of Invasions by Animals and Plants* (Methuen, London).
2. Vermeij, G. J. (1996) *Biological Conservation* **78,** 3–9.
3. Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. (1997) *Science* **277,** 494–499.
4. Sala, O. E., Chapin, F. S. I., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., *et al.* (2000) *Science* **287,** 1770–1774.
5. Williamson, M. (1996) *Biological Invasions* (Chapman and Hall, London).
6. Vitousek, P. M., D'Antonio, C. M., Loope, L. L. & Westbrooks, R. (1996) *Am. Sci.* **84,** 468–478.
7. Rahel, F. J. (2000) *Science* **288,** 854–856.
8. Mack, R. N. (1985) in *Studies in Plant Demography*, ed. White, J. (Academic, London), pp. 127–142.
9. Cohen, A. N. & Carlton, J. T. (1998) *Science* **279,** 555–558.
10. Nico, L. G. & Fuller, P. L. (1999) *Fisheries* **24,** 1–27.
11. Mack, R. N. (1981) *Agro-Ecosystems* **7,** 145–165.
12. Crooks, J. A. & Soule, M. E. (1999) in *Invasive Species and Biodiversity Management*, eds. Sandlund, O. T., Schei, P. J. & Viken, A. (Kluwer, Dordrecht, The Netherlands), pp. 103–125.
13. Por, F. D. (1978) *Lessepsian Migration* (Springer, Berlin).
14. Spanier, E. & Galil, B. S. (1991) *Endeavour* **15** (New Series), 102–106.
15. Golani, D. (1993) *Isr. J. Zool.* **39,** 391–402.
16. Simpson, G. G. (1980) *Splendid Isolation: The Curious History of South American Mammals* (Yale Univ. Press, New Haven, CT).
17. Webb, S. D. (1991) *Paleontology* **17,** 266–280.
18. Huey, R. B., Gilchrist, G. W., Carlson, M. L., Berrigan, D. & Serra, L. (2000) *Science* **287,** 308–309.
19. Ayala, F. J., Serra, L. & Prevosti, A. (1989) *Genome* **31,** 246–255.
20. Johnston, R. F. & Selander, R. K. (1960) *Evolution* **14,** 548–550.

21. Cody, M. L. & Overton, J. M. (1996) *J. Ecol.* **84,** 53–61.
22. Losos, J. B., Warheit, K. I. & Schoener, T. W. (1997) *Nature (London)* **387,** 70–73.
23. Britton-Davidian, J., Catalan, J., Ramalhinho, M. D., Ganem, G., Auffray, J. C., Capela, R., Biscoito, M., Searle, J. B. & Mathias, M. D. (2000) *Nature (London)* **403,** 158–158.
24. Easteal, S. (1985) *Evolution* **39,** 1065–1075.
25. Carroll, S. P. & Dingle, H. (1996) *Biol. Conserv.* **78,** 207–214.
26. Singer, M. C., Thomas, D. & Parmesan, C. (1993) *Nature (London)* **366,** 681–683.
27. Zimmerman, E. C. (1960) *Evolution* **14,** 137–138.
28. Harlan, J. R. (1965) *Euphytica* **14,** 173–176.
29. De Wet, J. M. J. & Harlan, J. R. (1975) *Econ. Bot.* **29,** 99–107.
30. Rhymer, J. M. & Simberloff, D. (1996) *Annu. Rev. Ecol. Syst.* **27,** 83–109.
31. McMillan, M. & Wilcove, D. (1994) *Update* **11,** 5–6.
32. Abernathy, K. (1994) *Mol. Ecol.* **3,** 551–562.
33. Echelle, A. A. & Echelle, A. F. (1997) *Conserv. Biol.* **11,** 153–161.
34. Lariagder, C. R. & Scholl, A. (1996) *Mol. Ecol.* **5,** 417–426.
35. Abbott, R. J. (1992) *Trends Ecol. Evol.* **7,** 401–405.
36. Anttila, C. K., Daehler, C. C., Rank, N. E. & Strong, D. R. (1998) *Am. J. Bot.* **85,** 1597–1601.
37. Levin, D. A., Francisco-Ortega, J. & Jansen, R. K. (1996) *Conserv. Biol.* **10,** 10–16.
38. Thompson, J. D. (1991) *BioScience* **41,** 393–401.
39. Gray, A. J. (1986) *Philos. Trans. R. Soc. London B* **314,** 655–674.
40. Holway, D. A. & Suarez, A. V. (1999) *Trends Ecol. Evol.* **14,** 328–330.
41. Townsend, C. R. (1996) *Biol. Conserv.* **78,** 13–22.
42. Blossey, B. & Notzold, R. (1995) *J. Ecol.* **83,** 887–889.
43. Willis, A. J., Thomas, M. B. & Lawton, J. H. (1999) *Oecologia* **120,** 632–640.
44. Crawley, M. J. (1987) in *Colonization, Succession and Stability*, eds. Gray, A. J., Crawley, M. J. & Edwards, P. J. (Blackwell, Oxford), pp. 429–453.
45. Noble, I. R. (1989) in *Biological Invasions*, eds. Drake, J. A., Mooney, H. A., di Castri, F., Groves, R. H., Kruger, F. J., Rejmanek, M. & Williamson, M. (Wiley, Chichester, U.K.), pp. 301–313.
46. Holway, D. A. (1999) *Ecology* **80,** 238–251.
47. Human, K. G. & Gordon, D. M. (1996) *Oecologia* **105,** 405–412.
48. Kenward, R. E. & Holm, J. L. (1993) *Proc. R. Soc. London Ser. B* **251,** 187–194.
49. Race, M. S. (1982) *Oecologia* **54,** 337–347.
50. Douglas, M. E., Marsh, P. C. & Minckley, W. L. (1994) *Copeia* **1994,** 9–19.
51. Porter, S. D. & Sagivnano, D. A. (1990) *Ecology* **71,** 2095–2106.
52. Petren, K. & Case, T. J. (1996) *Ecology* **77,** 118–132.
53. Byers, J. E. (2000) *Ecology* **81,** 1225–1239.
54. Dick, J. T. A., Elwood, R. W. & Montgomery, W. I. (1995) *Behav. Ecol. Sociobiol.* **37,** 393–398.
55. Carlton, J. T., Geller, J. B., Reaka-Kudla, M. L. & Norse, E. A. (1999) *Annu. Rev. Ecol. Syst.* **30,** 515–538.
56. Richardson, D. M., Allsopp, N., D'Antonio, C. M., Milton, C. M. & Rejmanek, M. (2000) *Biol. Rev. Camb. Philos. Soc.* **75,** 65–93.
57. Simberloff, D. & Von Holle, B. (1999) *Biol. Invasions* **1,** 21–32.
58. Bond, W. & Slingsby, P. (1984) *Ecology* **65,** 1031–1037.
59. Oldroyd, B. P. (1999) *Trends Ecol. Evol.* **14,** 293–332.
60. Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) *BioScience*, 607–615.
61. Rodda, G. H., Fritts, T. H. & Chiszar, D. (1977) *BioScience* **47,** 565–574.
62. Case, T. J. & Bolger, D. T. (1991) *Evol. Ecol.* **5,** 272–290.
63. Moyle, P. B. & Light, T. (1996) *Biol. Conserv.* **78,** 141–161.
64. Worthington, E. B., Lowe, M. C. & Connell, R. (1994) *Environ. Conserv.* **21,** 199–213.
65. Ricciardi, A. & Rasmussen, J. B. (1999) *Conserv. Biol.* **13,** 1220–1222.
66. Ricciardi, A., Neves, R. J. & Rasmussen, J. B. (1998) *J. Anim. Ecol.* **67,** 613–619.
67. Stone, R. (1999) *Science* **285,** 1837.
68. Strong, D. R. & Pemberton, R. W. (2000) *Science* **288,** 1969–1970.
69. Brown, J. H. (1995) *Macroecology* (Univ. of Chicago Press, Chicago).
70. McKinney, R. L. (1998) *Global Ecol. Biogeogr. Lett.* **7,** 297–301.

Rapid plant diversification: Planning for an evolutionary future

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Systematic conservation planning is a branch of conservation biology that seeks to identify spatially explicit options for the preservation of biodiversity. Alternative systems of conservation areas are predictions about effective ways of promoting the persistence of biodiversity; therefore, they should consider not only biodiversity pattern but also the ecological and evolutionary processes that maintain and generate species. Most research and application, however, has focused on pattern representation only. This paper outlines the development of a conservation system designed to preserve biodiversity pattern and process in the context of a rapidly changing environment. The study area is the Cape Floristic Region (CFR), a biodiversity hotspot of global significance, located in southwestern Africa. This region has experienced rapid (post-Pliocene) ecological diversification of many plant lineages; there are numerous genera with large clusters of closely related species (flocks) that have subdivided habitats at a very fine scale. The challenge is to design conservation systems that will preserve both the pattern of large numbers of species and various natural processes, including the potential for lineage turnover. We outline an approach for designing a system of conservation areas to incorporate the spatial components of the evolutionary processes that maintain and generate biodiversity in the CFR. We discuss the difficulty of assessing the requirements for pattern versus process representation in the face of ongoing threats to biodiversity, the difficulty of testing the predictions of alternative conservation systems, and the widespread need in conservation planning to incorporate and set targets for the spatial components (or surrogates) of processes.

There are numerous pleas in the literature for integrated systems of conservation areas that will maintain disturbance regimes, migratory corridors, habitat diversity, landscape connectivity, evolutionary templates, and other spatial features necessary for the maintenance of evolutionary processes (1–4). There has been some debate as to whether priority should be given to areas supporting ancestral taxa with evolutionary potential (5, 6) or those representing evolutionary fronts of currently speciating taxa (7–10). Recently, Moritz and coworkers (11) have used comparative phylogeography to identify areas that encompass both the adaptive and historical components of genetic diversity of vertebrates in the rainforests of northeastern Australia. However, there have been no studies that attempt to identify the spatial components of a wide spectrum of evolutionary processes or to set explicit targets for their protection in particular regions.

If we are to plan for an evolutionary future, then evolutionary processes—those that maintain genetic diversity and promote diversification—must be explicitly considered, and represented, in the conservation plan (1, 11, 12). This is not a trivial issue. There are very few places in the world, in particular in its endemic-rich and threatened regions (13), where evolutionary processes and their spatial components are understood well enough to be included in conservation planning. Over the past few decades, considerable insights have been gained regarding evolutionary processes in the Cape Floristic Region (CFR) of South Africa, especially for plants. Because the available data are representative of most plant lineages in the region, they provide a good basis for conservation planning.

In this paper, we provide a brief overview of evolutionary processes in the CFR, a species-rich region that is recognized as a global priority for conservation action (13). We focus in particular on rapid diversification of plant lineages. We then review briefly some recent developments in systematic conservation planning and the need to extend these ideas to apply not only to biodiversity pattern, but also to ecological and evolutionary processes. Because conservation planning is a spatially explicit exercise, even processes must be protected by their spatial components or surrogates. Accordingly, we describe a framework for planning for an evolutionary future in the CFR, identifying seven types of spatial components of evolutionary processes, setting explicit conservation targets for each, and outlining the development of a conservation plan to achieve these targets. We conclude by discussing the difficulty of testing predictions about biodiversity persistence deduced from alternative conservation plans, the contributions of the approach presented here, and its potential for widespread application.

Rapid Diversification in the CFR

Rapid diversification, often associated with key innovations and leading to flocks of species that show fine-scale habitat discrimination, has been reported for some plant lineages (26–28), especially on islands (29, 30), for Andean birds (9), and for fish, most notably the cichlids of the African Rift Lakes (19). Without a doubt, the distinctive evolutionary feature of the CFR is the recent and massive diversification of many plant lineages (20, 21). The region includes some 9,000 plant species in 90,000 km^2, 69% of which are endemic (21)—one of the highest concentrations of endemic plant species in the world (13). This diversity is concentrated in relatively few lineages that have radiated spectacularly. Thus, 13 genera (of a total of 988) each comprise more than 100 species, and together these account for 25% of all species in the flora (21). Similarly, of the region's 173 families, 12 each comprise more than 200 species and, in combination, include 64% of the CFR's flora.

Although the evidence is patchy, it seems certain that this massive diversification has occurred relatively recently, mostly after climatic deterioration in the late Pliocene when seasonal (Mediterranean-type) climates developed and recurrent fire became an important ecological factor (22, 23). That many lineages are in the midst of massive diversification events is suggested by the restriction of localized endemics to very young sediments (20), the large clusters of closely related species resulting in poor phylogenetic resolution in clades (24, 25), and

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Abbreviation: CFR, Cape Floristic Region.

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a very recent (post-Pleistocene) appearance in the pollen record of species-rich taxa, notably the Mesembryanthemaceae (26).

Diversification-prone lineages in the CFR are not a random assemblage either biologically or ecologically. Generally, component species among woody groups are low, fire-killed (i.e., nonsprouting) shrubs with poorly dispersed seeds, small and weakly persistent seed banks, and insect-pollinated flowers (21, 27, 28). These traits, especially fire sensitivity, which could be regarded as a key innovation (in the sense of ref. 29; see also refs. 22 and 27), have favored increased diversification rates. Thus, fire-induced plant mortality increases generation turnover, thereby providing potential for more rapid evolution than sprouters (compare refs. 27 and 30). Small and weakly persistent seed banks, in combination with fire sensitivity, result in nonoverlapping generations, thereby increasing the probability of the manifestation of genetic novelties associated with each generation, as well as increasing the probability of population fragmentation via fire-induced local extinction (22, 27). Finally, restricted gene flow, a consequence of short-distance seed dispersal and insect pollination, promotes isolation and hence diversification of populations in different habitats (31, 32).

A simple microgeographic speciation model applies (28): subpopulations of common species, presumably with considerable genetic diversity, are isolated geographically by fire-induced local extinction or climate change, on the periphery of the parent population in a different habitat. This process can occur very rapidly (even after a single fire) and, owing to limited gene flow, over small spatial scales. In these isolated populations, a combination of chance fixation of new genes and strong selection in a different habitat results in rapid speciation. Predictably, the overwhelming majority of range-restricted, terminal taxa are habitat, principally edaphic, specialists (20, 27, 33, 35), implying a strong ecological component to the diversification processes (21, 31, 34).

Adaptation to pollinators has also played a major role in the diversification of the CFR's flora (35). This is especially true of the region's large geophyte flora (*ca.* 1,500 species) where specialist pollinators have driven speciation in several groups (e.g., refs. 36–38). Strong selection for specialist pollinators is presumably a consequence of the scarcity of pollinators and widespread pollen limitation in the infertile and fire-prone CFR landscapes (39). However, ecological factors, especially soil type, may nonetheless play an overriding role in speciation amongst geophytes, as in the irid genus *Lapeirousia* (33).

Diversification of the CFR biota has also occurred in relation to meso- and macroscale ecological gradients, also operating over larger temporal scales than those described above. These larger processes are the consequence of geographic isolation driven by oscillating climate change during the Pleistocene (21, 40). There is some evidence for ecological diversification of both plant and invertebrate lineages in relation to the high environmental diversity associated with lowland–upland gradients (6, 34, 41). Riverine systems that breach montane migration barriers, thereby linking dry interior basins with mesic coastal forelands, are important for migration and exchange between these biotas: subsequent isolation of populations may also play a role in speciation (42). Plants and invertebrates have also diversified across the macroclimatic gradients evident in the CFR (41, 43). There may also be as yet undisclosed levels of within-species genetic variation between geographically isolated parts of the CFR.

Further rapid climate change is likely to cause the extinction of many of the range-restricted and habitat-specialist members of the actively speciating flocks in the CFR (44–47). However, by changing habitat characteristics and promoting population isolation, climate change may also enhance turnover of actively diversifying lineages. Another widespread influence is ongoing transformation of habitats to intensive uses. The challenge for conservation planning is, therefore, to create conditions that enable evolutionary processes to continue in a rapidly changing world (48).

Systematic Conservation Planning

Conservation planning is a branch of conservation biology that seeks to identify spatially explicit options for the preservation of biodiversity (49, 50). Alternative systems of conservation areas are, in essence, hypotheses about effective ways of promoting the persistence of biodiversity. It is vital, therefore, that planning considers not only the representation of populations, species, and other components of biodiversity pattern, but also—as we argue below—the processes that underpin these patterns. In order for these processes to be represented in a conservation plan, they must be explicitly identified by their spatial components [e.g., a particular physiographical gradient across which lineages have diversified (9, 12)].

Invariably, the conservation options arising from a plan are constrained by a number of factors, such as the existing reserve system (51), the extent and configuration of transformed habitat (52), and forms of land use that are financially more viable (at least in the short term) than conservation (53). To be effective, conservation planning should be systematic. Systematic approaches share the following features: they are data-driven; target-directed; efficient; explicit, transparent, and repeatable; and flexible (12, 54).

A map of irreplaceability, such as the one shown in Fig. 1, is an outcome of a systematic approach that presents options for planning new protected areas (55). Essentially, irreplaceability is a measure assigned to an area that reflects its importance, in the context of the planning domain (e.g., the CFR), for achieving a set of regional conservation targets (e.g., a specified extent of each habitat type). Irreplaceability can be defined in two ways (57): the likelihood of an area being required to achieve the set of conservation targets for the region; and the extent to which the options for achieving a system of conservation areas that is representative (achieves all of the conservation targets) is reduced if that area is lost or made unavailable.

In areas of high irreplaceability, all or most extant habitat is required to achieve targets; in areas of low irreplaceability, there is greater flexibility in the array of available areas required to meet regional conservation targets (55). In the case of the CFR (Fig. 1), the broad pattern of irreplaceability is largely driven by agricultural transformation. Areas comprising habitat types that have been almost entirely transformed—mainly renosterveld and allied shrublands of the coastal lowlands (58)—have maximum irreplaceability. All extant occurrences of these habitats are required to fulfill the conservation target, and options for protected area establishment, or some form of conservation action, are severely constrained. In contrast, sites that include habitats associated with remote and infertile mountain landscapes, which are in a largely pristine state and where most protected areas are located (59), have low irreplaceability: here there are numerous options to meet the outstanding conservation targets.

Although the analysis in Fig. 1 provides a solid base for systematic conservation planning, it has a major limitation. The outcome reflects the options for achieving targets for pattern only. The representation of biodiversity pattern (species, habitats, etc.) is only one component of an effective conservation plan; an explicit consideration of the evolutionary processes that will maintain biodiversity in the long term is also required (11, 12), especially in a world that is increasingly threatened by habitat loss and climate change (44, 45).

Planning for Ecological and Evolutionary Processes

The past 20 years have seen the development of systematic conservation protocols that identify whole sets of complementary areas that collectively achieve some overall conservation goal—the "minimum set" approach (49, 60). In this strategy, the

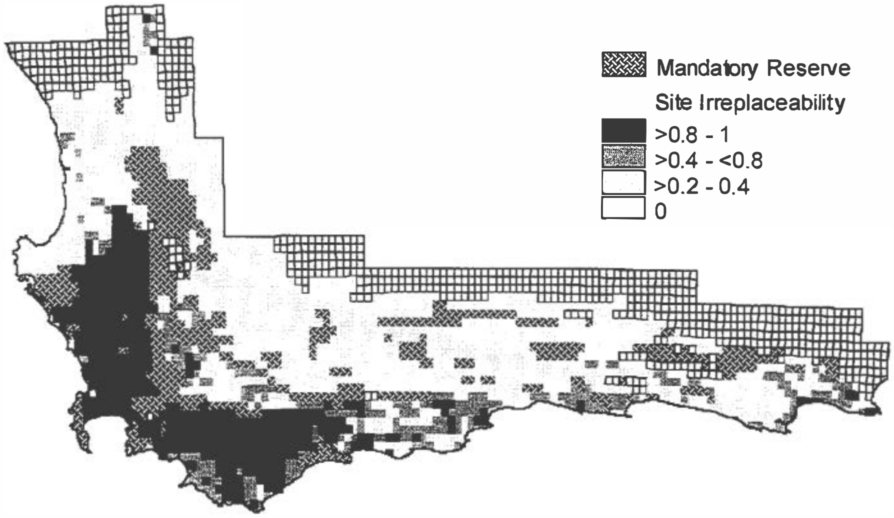

Fig. 1. A map of site irreplaceability for the CFR. Areas (planning units comprising 1/16° cells) where existing reserves cover >50% of the area are regarded as mandatory reserves. Totally irreplaceable units include areas of habitat that are essential to meet reservation targets, whereas units where irreplaceability is zero comprise habitat for which reservation targets have been achieved. The analysis, driven by explicit reservation targets for 88 Broad Habitat Units (BHUs), and mapped at 1:250,000 (56), was undertaken by using C-PLAN, a decision support system linked to a geographic information system (53).

conservation goal consists of quantitative targets for each species (e.g., at least one occurrence) or each habitat (e.g., at least 10% of its total area). The aim is to represent the required amount of each species or habitat in as small an area as possible. Usually, rapid implementation of the reserve system is assumed implicitly, so there is no basis for deciding how to schedule conservation action among the selected areas in relation to prevailing threats.

A more realistic scenario, however, is for implementation of the reserve system to take years or decades, during which time the agents of biodiversity loss continue to operate. In such situations, strategies for maximizing representation on paper must be complemented or replaced by those that maximize "retention" in the face of ongoing loss or degradation of habitat. A crucial consideration in maximizing retention is the assignment of priorities based on the irreplaceability of a site and its vulnerability to biodiversity loss as a result of current or impending threatening processes (61). In this scenario, areas with high irreplaceability and high vulnerability are the highest priorities for conservation action. The objective of the approach is to minimize the extent to which representation targets are compromised by ongoing loss of habitat and species. The same rationale underlies some approaches to identifying conservation areas globally (13).

A further step is needed, however, for conservation planning to truly address the long-term persistence of biodiversity. The implementation of reserve systems that are designed to retain only biodiversity pattern will not ensure long-term conservation. This is because these systems do not explicitly consider the ecological and evolutionary processes that maintain and generate biodiversity (1, 3, 11, 12, 62). The ultimate goal of conservation planning should be the design of systems that enable biodiversity to persist in the face of natural and human-induced change. Design is defined here as the size, shape, connectivity, orientation, and juxtaposition of conservation areas intended to address issues such as viable populations, minimization of edge effects, maintenance of disturbance regimes and movement patterns, continuation of evolutionary processes, and resilience to climate change.

Given that the implementation of reserve systems is almost always gradual, and accompanied by ongoing loss of habitat, the conservation of both pattern and process will require two things: consideration of representation and design in the identification of potential conservation areas; and sound decisions about the progressive implementation of conservation action so that land use and other threats have minimal impact on the desired outcome.

In the implementation phase of a reserve system designed for retention and persistence, the importance of threatening processes in compromising the achievement of both pattern and process goals will need to be considered and balanced (12). This strategy should achieve greater long-term benefits for biodiversity than strategies based only on the representation of pattern.

Planning for an Evolutionary Future in the CFR

Because conservation planning is a spatial exercise, an essential requirement of planning for the maintenance of natural processes is the identification of the spatial components of those processes—examples are habitat gradients or geographical barriers that are associated with lineage turnover. To our knowledge, no studies have integrated these spatial requirements into a conservation plan. This we are attempting to do in a current exercise for the CFR.

On the basis of our present understanding of diversification processes in the CFR, we identified seven spatial components to be protected to promote ongoing evolution and set targets for each (Table 1). These targets can be used to produce a map of irreplaceability for evolutionary processes but, in the overall conservation plan, are combined with requirements for representing biodiversity pattern and the continuation of various ecological processes. The next step was to design a system of conservation areas by selecting from areas that contain one or more of the spatial components in Table 1. The options associated with the selection of areas were constrained by several factors, including a pragmatic requirement to incorporate the existing reserve system; the avoidance of excessively transformed areas; and the need to select, where possible, areas also with high irreplaceability for targets for biodiversity pattern. In many instances, especially in lowland regions, habitats are so extensively transformed that it is no longer possible to achieve process targets—the evolutionary future of the CFR has already been severely compromised.

Fig. 2 shows the sequential assembly of the conservation system designed to achieve evolutionary process targets in the CFR. The rule applied for the design sequence was to initially attempt to achieve targets for which there were limited options

Table 1. Spatial components of evolutionary processes in the CFR

Spatial component	Method of identification	Target	Key evolutionary process conserved
Juxtaposed edaphically different habitats	Identify planning units with particular combinations of Broad Habitat Units (56) that reflect strong edaphic contrasts (limestone and adjacent acidic substrata) known to be associated with plant diversification processes. Exclude "unsuitable" planning units based on fragmentation of native vegetation and lack of contiguity with other units.	At least one example of each specified combination of Broad Habitat Units in each major climatic zone.	Ecological diversification of plant lineages in relation to fine-scale edaphic gradients (20).
Entire sand movement corridors	Identify planning units containing the three specific dune pioneer habitats. Exclude any corridors (sediment-sources) with limited conservation potential of surrounding land (particularly in the sediment-sink or downwind zones). Assume stands of dense alien plants make corridors irrecoverable.	At least one entire corridor of each type.	Ecological diversification of plant lineages in relation to fine-scale edaphic gradients (20).
Whole riverine corridors	Identify major rivers that link inland basins with coastal plains. Identify untransformed corridors or parts of corridors.	All of any intact, or the untransformed parts of each of the major corridors (five river systems; ten river corridors).	Migration and exchange between inland and coastal biotas (42).
Gradients from uplands to coastal lowlands and interior basins	Identify planning units on the following interfaces of upland and lowland: Coastal range/coastal plain Coastal range/interior basin Inland range/interior basin Inland range/Karoo basin which would allow the construction of corridors between these landscapes.	At least one example of each gradient within each of the major climate zones (9). Gradients width must encompass at least one untransformed planning unit and maximize climatic heterogeneity.	Ecological diversification of plant and animal lineages in relation to steep environmental gradients (6, 34, 41).
Macro-scale climatic gradients	Complement gradients between lowlands and uplands (meso scale) with macro-scale connectivity in two main directions: North–south in the western CFR along both the coastal forelands and inland mountains; East–west in the southern and eastern CFR along coastal forelands, coastal mountains, interior basins, and interior mountains.	Unbroken transects along all of the geographical gradients.	Geographical diversification of plant and animal lineages in relation to macroclimatic gradients (56, 58).
Mega wilderness areas	Identify contiguous planning units that encompass ca 500,000 ha of untransformed habitat, transcend biome boundaries (63), and include all or part of a riverine corridor.	One in the northwestern, one in the southern, and one in the southeastern CFR.	Maintenance of all evolutionary processes, including predator–prey processes involving top predators (59).
Transitions between major Broad Habitat Unit categories (56) and biome boundaries.	Where possible, expand conservation areas to encompass these transitions.	As many transitions as possible.	Exchange between phylogenetically distinct biotas.

The components need to be identified geographically and given quantitative targets for conservation planning. The term "planning units" refers to areas used in our current planning exercise as the preliminary building blocks of an expanded system of conservation areas. They are 1/16° grid cells each covering about 4,000 ha. About 2,510 planning units cover the whole CFR.

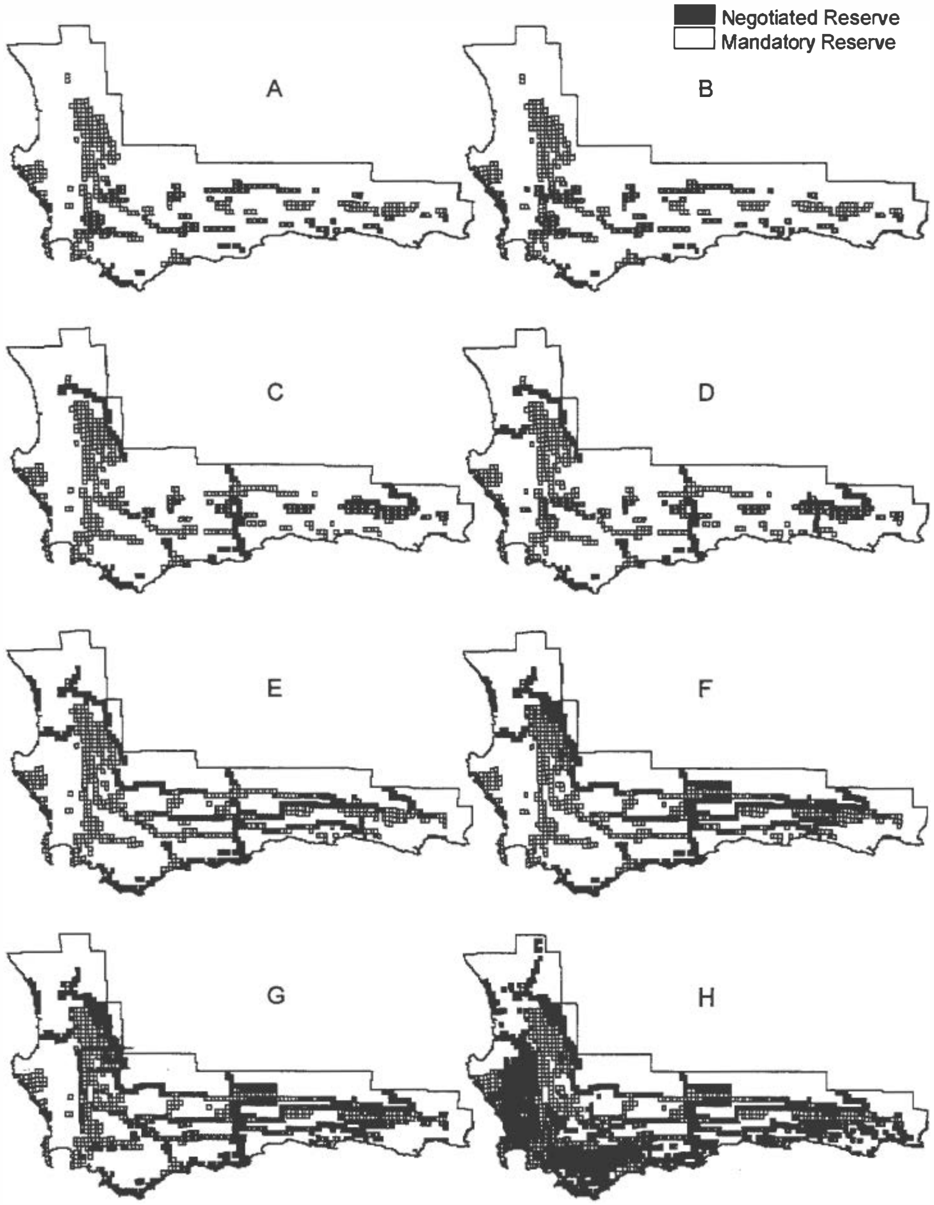

Fig. 2. Stages in the design of a system of conservation areas for the CFR that will achieve targets for biodiversity pattern and ecological and evolutionary processes. (*A*) juxtaposed edaphically different habitats; (*B*) entire sand movement corridors; (*C*) whole riverine corridors; (*D*) upland–lowland gradients; (*E*) macroclimatic gradients; (*F*) mega wilderness areas; (*G*) major biological transitions not identified in stages *A–F*; and (*H*) an additional minimum set of areas required to achieve all pattern targets. The minimum set was identified by using a reserve selection algorithm driven by irreplaceability (53).

(e.g., unique combinations of edaphic substrata), proceeding to targets offering greater flexibility in terms of spatial location. Particular attention was given to achieving more than one target within any one notional reserve. Nonetheless, the overall system depicted in Fig. 2 is one of several options for conserving processes and is accordingly presented as an example of the approach that we have used. Areas contributing to process targets were selected in the C-PLAN software system (53) as negotiated reserves, whereas the existing reserve system is depicted as mandatory reserves. The mandatory reserves, however, do not contribute substantially to achieving process targets. Of the total area selected to achieve the targets, only 41% was contributed by the existing reserve system, and the area contribution of this system to each of the seven spatial components ranged from 0–48%. Thus, in addition to being another example of an ad hoc reserve system that is inadequate in terms of pattern representation (ref. 59; see also ref. 51), extant CFR reserves are not located in a manner that will sustain evolutionary processes.

The components identified in Table 1 comprise the spatial requirements of evolutionary processes at many spatial scales. The planning units themselves, each comprising about 4,000 ha, are sufficiently large to sustain regular, whole-patch fires (64), a disturbance essential for the maintenance of key evolutionary processes (22), to maintain plant and insect biodiversity (65–67), and to maintain plant–insect pollinator relations (67, 68). However, larger areas of juxtaposed habitat encompassing the spatial components of evolutionary processes that operate over meso- and macroscale ecological gradients, are required to ensure the long-term persistence of biodiversity in the CFR. Accordingly, we hypothesize that the system identified in Fig. 2 will ensure ongoing diversification in the CFR by conserving the spatial components of key evolutionary processes. The maintenance of juxtaposed habitats over different spatial scales should impart a measure of resilience to impending climate change (44), which is predicted to have a substantial effect on the flora and vegetation of the CFR (69).

A key issue in conservation planning is the scheduling of conservation action on the ground, requiring choices in both space and time (61). In principle, irreplaceability and vulnerability to threatening processes should guide priorities for implementation: action should minimize the extent to which conservation targets are compromised before conservation management is applied (61). However, when conservation targets deal with the representation of both pattern and process, as is the case for this study, there are no established ways of comparing the relative risks of alternative approaches to implementation. For example, how should the outright loss of an extensively transformed and fragmented habitat be compared with the loss of a section of climatic gradient, comprising adequately conserved habitat but essential for sustaining evolutionary processes? Resolving these conflicts is a major challenge for conservation planning (12), and is the subject of ongoing research. A key contribution is the establishment of irreplaceability maps for the achievement of process targets.

Discussion and Conclusions

The system of conservation areas identified in Fig. 2 represents a set of hypotheses about the maintenance biodiversity and ongoing diversification in the CFR. The major prediction is that this system will maintain more biodiversity in the long term than alternative systems based on pattern representation only (12). It is not feasible, ethically or practically, to test this prediction: the scale and nature of the problem rule out experiments. We can, however, monitor and, where possible, adjust the design as results and more data become available; although, given the rapid escalation of all components of global change, time is not on our side (9, 11).

The contributions of the conservation planning approach that we have used for the CFR are the spatial identification of evolutionary drivers and the setting of explicit targets for these spatial components. Furthermore, in the larger project described partially here, these considerations are being integrated more thoroughly than shown in this indicative and preliminary account. The larger study will also have to face difficult tradeoffs between the representation of pattern and process, as well as between requirements for biodiversity conservation and other socioeconomic considerations. There are no easy answers for resolving these conflicts, nor can they be ignored.

Finally, the concepts and analytical techniques used in this study are of general applicability. The big challenge for all regions is to identify the spatial components of evolutionary processes and set targets for these. Biodiversity is being lost everywhere at an alarming rate. The current focus on pattern representation in conservation planning will only temporarily slow the rate of extinction. It is vitally important to plan for evolutionary futures everywhere.

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1. Frankel, O. H. (1974) *Genetics* **78,** 53–65.
2. Pickett, S. T. A. & Thompson, J. N. (1978) *Biol. Conserv.* **13,** 27–37.
3. Hunter, M. L., Jacobsen, G. L. & Webb, T. (1988) *Conserv. Biol.* **2,** 375–385.
4. Harris, L. D. & Cropper, W. P., Jr. (1992) in *Global Warming and Biological Diversity*, eds. Peters, R. L. & Lovejoy, T. E. (Yale Univ. Press, New Haven, CT), pp. 309–324.
5. Williams, P. H., Humphries, C. J. & Vane-Wright, R. I. (1991) *Aust. Syst. Bot.* **4,** 665–679.
6. Linder, H. P. (1995) *Conserv. Biol.* **9,** 585–595.
7. Erwin, T. L. (1991) *Science* **253,** 750–752.
8. Brooks, D. R., Mayden, R. L. & McLennan, D. A. (1992) *Trends Ecol. Evol.* **7,** 55–59.
9. Fjeldså, J. (1994) *Biodiv. Conserv.* **3,** 207–226.
10. Moritz, C. (1995) *Philos. Trans. R. Soc. London* **349,** 113–118.
11. Moritz, C. (1999) in *The Biology of Biodiversity*, ed. Kato, M. (Springer–Verlag, Tokyo), pp. 21–34.
12. Cowling, R. M., Pressey, R. L., Lombard, A. T., Demet, P. G. & Ellis, A. G. (1999) *Diversity Distrib.* **5,** 51–71.
13. Myers, N., Mittermeier, R. A., Mittermeier, C. G. & da Fonseca, G. A. B. (2000) *Nature (London)* **403,** 853–858.
14. Hodges, S. A. & Arnold, M. L. (1994) *Proc. Natl. Acad. Sci. USA* **91,** 5129–5132.
15. Rieseberg, L. H., Beckstrom-Sternberg, S. M., Liston, A. & Arias, D. M. (1991) *Syst. Bot.* **16,** 50–76.
16. Schwarzbach, A. E. & Kadereit, J. W. (1995) *Plant Syst. Evol.* **9,** 159–170.
17. Stuessy, T. F., Crawford, D. J. & Marticorena, C. (1990) *Syst. Bot.* **15,** 338–346.
18. Baldwin, B. G. & Carr, G. D. (1991) *Proc. Natl. Acad. Sci USA* **88,** 1840–1843.
19. Galis, F. & Metz, J. J. (1998) *Trends Ecol. Evol.* **13,** 1–2.
20. Cowling, R. M. & Holmes, P. M. (1992) *Biol. J. Linn. Soc.* **47,** 367–383.
21. Goldblatt, P. & Manning, J. (2000) *Strelitzia* **9,** 1–744.
22. Cowling, R. M. (1987) *S. Afr. J. Sci.* **83,** 106–111.
23. Linder, H. P., Meadows, M. E. & Cowling, R. M. (1992) in *The Ecology of Fynbos: Nutrients, Fire and Diversity*, ed. Cowling, R. M. (Oxford Univ. Press, Cape Town, South Africa), pp. 113–124.
24. Ihlenfeldt, H.-D. (1994) *Annu. Rev. Ecol. Syst.* **25,** 521–546.
25. Oliver, E. G. H. (1991) *Contrib. Bolus Herbarium* **13,** 158–208.
26. Cowling, R. M., Rundel, P. W., Desmet, P. G. & Esler, K. J. (1998) *Diversity Distrib.* **4,** 27–36.
27. Schutte, A. L., Vlok, J. H. J. & van Wyk, B.-E. (1995) *Pl. Syst. Evol.* **195,** 243–259.
28. Cowling, R. M. & Lamont, B. B. (1998) *Aust. J. Bot.* **46,** 335–355.
29. Heard, S. B. & Hauser, D. L. (1995) *Hist. Biol.* **10,** 151–173.
30. Marzluff, J. M. & Dial, K. P. (1991) *Ecology* **72,** 428–439.
31. Linder, H. P. (1985) in *Species and Speciation*, ed. Vrba, E. S. (Transvaal Museum, Pretoria, South Africa), pp. 53–57.
32. Slingsby, P. & Bond, W. J. (1985) *S. Afr. J. Bot.* **51,** 30–35.
33. Goldblatt, P. & Manning, J. C. (1996) *Ann. Mo. Bot. Gard.* **83,** 346–361.
34. Linder, H. P. & Vlok, J. (1991) *Pl. Syst. Evol.* **175,** 139–160.
35. Johnson, S. J. (1996) *Taxon* **45,** 59–66.
36. Johnson, S. J. (1997) *Bot. J. Linn. Soc.* **123,** 225–235.
37. Johnson, S. J. & Steiner, K. E. (1997) *Evolution* **51,** 45–53.
38. Manning, J. C. & Goldblatt, P. (1996) *Ann. Mo. Bot. Gard.* **83,** 67–86.
39. Johnson, S. J. & Bond, W. J. (1997) *Oecologia* **109,** 530–534.
40. Rourke, J. P. (1972) *J. S. Afr. Bot.* **8,** Suppl., 1–184.
41. Enrödy-Younga, S. (1988) *Ann. S. Afr. Mus.* **96,** 359–424.
42. Geldenhuys, C. J. (1997) *Bothalia* **27,** 57–74.
43. Linder, H. P. & Mann, D. M. (1998) *Bot. J. Linn. Soc.* **128,** 319–357.
44. Peters, R. L. & Lovejoy, T. E., eds. (1992) *Global Warming and Biological Diversity* (Yale Univ. Press, New Haven, CT).
45. Rutherford, M. C., Powrie, L. W. & Schulze, R. E. (1999) *Diversity Distrib.* **5,** 253–262.
46. Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. (1995) *Science* **269,** 347–350.
47. Mckinney, M. L. (1997) *Annu. Rev. Ecol. Syst.* **28,** 495–516.
48. Lawton, J. H. (1997) *Oikos* **79,** 3–5.
49. Pressey, R. L., Humphries, C. J., Margules, C. R., Vane-Wright, R. I. & Williams, P. H. (1993) *Trends Ecol. Evol.* **8,** 124–128.
50. Williams, P. H., Prance, G. T., Humphries, C. J. & Edwards, K. S. (1996) *Biol. J. Linn. Soc.* **58,** 125–157.
51. Pressey, R. L. (1994) *Conserv. Biol.* **8,** 662–668.
52. Lombard, A. T., Cowling, R. M., Pressey, R. L. & Mustart, P. J. (1997) *Conserv. Biol.* **11,** 1101–1116.
53. Ferrier, S., Pressey, R. L. & Barret, T. (2000) *Biol. Conserv.* **93,** 303–325.
54. Pressey, R. L. (1999) *Parks* **9,** 1–6.
55. Pressey, R. L. (1999) *Parks* **5,** 41–51.
56. Cowling, R. M. & Heijnis, C. E. (2001) *S. Afr. J. Bot.* **67,** 15–38.
57. Pressey, R. L., Johnson, I. R. & Wilson, P. D. (1994) *Biodiv. Conserv.* **3,** 242–262.
58. Kemper, J., Cowling, R. M., Richardson, D. M., Forsyth, G. C. & McKelly, D. H. (2000) *Aust. J. Ecol.* **25,** 179–186.
59. Rebelo, A. G. (1992) in *The Ecology of Fynbos: Nutrients, Fire and Diversity*, ed. Cowling, R. M. (Oxford Univ. Press, Cape Town, South Africa), pp. 309–344.
60. Kirkpatrick, J. B. (1983) *Biol. Conserv.* **25,** 127–134.
61. Pressey, R. L., Ferrier, S., Hager, T. C., Woods, C. A., Tully, S. L. & Weiman, K. M. (1996) *For. Ecol. Mgmt.* **85,** 311–333.
62. Thompson, J. N. (1996) *Trends Ecol. Evol.* **11,** 301–303.
63. Rutherford, M. C. & Westfall, R. F. (1986) *Mem. Bot. Surv. S. Afr.* **54,** 1–45.
64. Donaldson, J. S., Nänni, I., Kemper, J. & Zachariades, C. (2000) *Conserv. Biol.*, in press.
65. Cowling, R. M. & Bond, W. J. (1991) *Biol. Conserv.* **55,** 243–256.
66. Kemper, J., Cowling, R. M. & Richardson, D. M. (1999) *Biol. Conserv.* **90,** 103–111.
67. Bond, W. J., Midgley, J. J. & Vlok, J. (1988) *Oecologia* **77,** 512–521.
68. Steiner, K. E. (1998) *Am. J. Bot.* **85,** 1180–1193.
69. Rutherford, M. C., O'Callaghan, M., Hurford, J. L., Powrie, L. W., Schulze, R. E., Kunz, R. P., Davis, G. W., Hoffman, M. T. & Mack, F. (1995) *J. Biogeog.* **22,** 523–531.

Human-modified ecosystems and future evolution

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Our global impact is finally receiving the scientific attention it deserves. The outcome will largely determine the future course of evolution. Human-modified ecosystems are shaped by our activities and their side effects. They share a common set of traits including simplified food webs, landscape homogenization, and high nutrient and energy inputs. Ecosystem simplification is the ecological hallmark of humanity and the reason for our evolutionary success. However, the side effects of our profligacy and poor resource practices are now so pervasive as to threaten our future no less than that of biological diversity itself. This article looks at human impact on ecosystems and the consequences for evolution. It concludes that future evolution will be shaped by our awareness of the global threats, our willingness to take action, and our ability to do so. Our ability is presently hampered by several factors, including the poor state of ecosystem and planetary knowledge, ignorance of human impact, lack of guidelines for sustainability, and a paucity of good policies, practices, and incentives for adopting those guidelines in daily life. Conservation philosophy, science, and practice must be framed against the reality of human-dominated ecosystems, rather than the separation of humanity and nature underlying the modern conservation movement. The steps scientists can take to imbed science in conservation and conservation in the societal process affecting the future of ecosystems and human well-being are discussed.

The Globalization of Human Impact

> Ecologists traditionally have sought to study pristine ecosystems to try to get at the workings of nature without the confounding influences of human activity. But that approach is collapsing in the wake of scientist's realization that there are no places left on Earth that don't fall under humanity's shadow.
>
> Richard Gallagher and Betsy Carpenter (1)

These opening remarks to *Science* magazine's special issue on Human-Dominated Ecosystems are long overdue. George Marsh (2) wrote his classic book *Man and Nature; or Physical Geography as Modified by Human Action* in 1864, before Haeckel (3) coined the word ecology and three quarters of a century before Tansley (4) gave us the ecosystem concept.

Ecologists' preoccupation with the pristine reflects a long tradition in western culture and a philosophy of separating humanity and nature (5), not to mention the humanities and science (6). The separation spilled over into conservation with its emphasis on setting aside pristine fragments of nature. Consequently, ecologists' recognition of the inseparability of human and natural realms could not be timelier in helping to bridge historical schisms, fostering sustainable development (7), and giving ecologists a new tool for investigating ecosystem processes (8).

Drawing a sharp line between the human and natural realms serves no purpose when our imprint is as ancient as it is pervasive. In the last few hundred thousand years, hunting and fire have shaped animal and plant communities across Africa (9). By the late Pleistocene, our shadow fell over every major landmass except Antarctica (10). The New World and Australia lost over two-thirds of their megafauna (>44 kg in body weight) within the last 10 to 50 millennia, and oceanic islands 50 to 90% of their birds in the last 3,000 years, largely because of human colonization and overkill (11). By the 20th century 40 to 50% of the world's land surface had been visibly transformed for domestic production and settlement (12). As we enter the 21st century, the earth's atmosphere, waters, and soils have been altered by human activity to the point of changing biogeochemical cycles and climate on a global scale (13).

What can we say about future evolution in a human-dominated world? We were invited to speculate freely. I suspect ecologists are uneasy about speculation because of their eschewal of human activity. I share the same uneasiness despite having studied humans as an integral part of African ecosystems for over three decades (14). But my uneasiness stems from a different concern—how little the fossil record can tell us about the future evolution because the future depends so much on human behavior. If we can't predict next year's economy, what can we say about evolution a thousand years from now, let alone millions?

Despite predictions of a mass extinction (15), the outcome is not inevitable. Human-induced extinctions are qualitatively different from previous mass extinctions (16). The threat is intrinsic, arising from a single species rather than an asteroid, volcanic activity, or other extrinsic agents. And, even though we can assume that human activity will affect future evolution by default or design, there is a world of difference between the two. Predictions based on past trends paint a bleak picture for our own species, let alone biodiversity. Yet even modest changes in fertility over the coming decades could see population growth level off (17). Ironically, scientists can change the course of evolution by persuading society to disprove their dire predictions! If my two cents worth helps, then I'm prepared to speculate in the interests of self-negation.

In reviewing human-dominated ecosystems I look at a number of interrelated topics. Each is vast and the subject of many reviews. These include ecosystem consequences of human impact (18–20), the consequences for humanity itself (7, 21), science applied to conservation (22), and science and conservation in society (23). My interest is not so much in the details as it is in showing the links and feedbacks among science, conservation, and society needed to avoid a dull homogenous planet fine for weeds and pathogens but not for the diversity of life or humankind.

Characteristics of Human-Dominated Ecosystems

Human impact on ecosystems can be looked at in several ways. Marsh (2), Tolba *et al.* (19), Heyward (19), and Vitousek *et al.* (12), for example, look at the outcome of using such measures as changes in habitat, species composition, physical characteristic, and biogeochemical cycles. Diamond (24) looks at the cause—the Evil Quartet of overkill, habitat destruction and

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Table 1. Some characteristics of intentionally modified ecosystems

High natural resource extraction
Short food chains
Food web simplification
Habitat homogeneity
Landscape homogeneity
Heavy use of herbicides, pesticides, and insecticides
Large importation of nonsolar energy
Large importation of nutrient supplements
Convergent soil characteristics
Modified hydrological cycles
Reduced biotic and physical disturbance regimes
Global mobility of people, goods, and services

fragmentation, impact of introduced species, and chains of extinction. Clarke and Munn (21) use systems models to explore human impact on ecosystems and its ramifications (19).

Although each approach has merit, none deals with motive. Did we create anthropogenic environments intentionally or not? Do they fulfill human goals? Ecologists are quick to judge the result without looking at cause, implying that we destroy nature without thought to the outcome. But, is our behavior really that aberrant? Would other species behave differently in the same situation?

I raise these questions because ignoring cause blinds us to the reasons for ecosystem modification. It also runs counter to the evolutionary perspective biologists apply to other species. What are the life-history and evolutionary strategies of *Homo sapiens*? How successful is that strategy in survival and reproductive terms? What are the costs? For consistency, we should look at human behavior as we do other species. After all, many, perhaps most, species modify their environment. Examples range from the crown-of-thorns starfish (25) to elephants (26). Problems of species overabundance, population crash, and ecological change are widely documented (27).

With these questions in mind, I have categorized human impact as either intended or unintended, fully recognizing the murky dividing line. My reason is 2-fold. First, the most universal and ancient features of "humanscapes" (28) arise from a conscious strategy to improve food supplies, provisions, safety, and comfort—or perhaps to create landscapes we prefer, given our savanna ancestry (29). The domestication of species, the creation of open fields, the raising of crops, and the building of shelters and settlements are the most obvious of intentional human activities, each practiced for millennia. Table 1 lists some ecosystem traits arising from deliberate human alteration of ecosystems. All of these characteristics are deliberate strategies to boost production and reproduction. As an evolutionary strategy, our success at commandeering resources and transforming the landscape to meet our needs has been phenomenal. Our numbers have grown from fewer than 4 million 10,000 years ago (30) to 6 billion today. Survival rates have risen, lifespan increased, and other indices of welfare improved in the evolutionary blink of an eye (18, 19).

But what of the negative consequences? Table 2 lists a few of the side effects. It can be argued that ecological side effects are not unique either, but stem from density-dependent effects widely reported in other species (27). The distinction between humans and other species thus lies not in our evolutionary strategy *per se*, but in the side effects or our global dominance. What then can be said about the consequences for ecosystems, evolution, and humans themselves?

Ecosystem Consequences

The more obvious consequences of human activity, such as the loss of species diversity and wild habitat, accelerated erosion, and sedimentation, have been extensively quantified (19, 20) and need no further elaboration. Harder to gauge are the consequences of human impact on such ecosystem properties as energy pathways, nutrient cycles, productivity, albedo, and, ultimately, the large-scale processes governing climate, hydrology, and biogeochemial cycles (31). The uncertainties over how human impact will affect large-scale ecosystem properties in turn clouds the evolutionary predictions we can make based on such species characteristics as ecological niche, demography, and adaptability.

Table 2. Some ecosystem side effects of human activity

Habitat and species loss (including conservation areas)
Truncated ecological gradients
Reduced ecotones
Low alpha diversity
Loss of soil fauna
Simplified predator–prey, herbivore–carnivore, and host–parasite networks
Low internal regulation of ecosystems due to loss of keystone agents
Side effects of fertilizers, pesticides, insecticides, and herbicides
Invasive nonindigenous species, especially weeds and pests
Proliferation of resistant strains of organism
New and virile infectious diseases
Genetic loss of wild and domestic species
Overharvesting of renewable natural resources
High soil surface exposure and elevated albedo
Accelerated erosion
Nutrient leaching and eutrophication
Pollution from domestic and commercial wastes
Ecological impact of toxins and carcinogenic emissions
Atmospheric and water pollution
Global changes in lithosphere, hydrosphere, atmosphere, and climate

An assessment of the ecosystem consequences is complicated by the question of the best measure. Should we use structural characteristics such as overall diversity, species composition, size-frequency, food web complexity, or trophic structure? Are ecological processes, whether resistance, resilience, perturbation, or some other measure more appropriate? Or should we use ecological functions such as overall productivity, water and nutrient cycles, and reflectance?

Here, rather than using a single measure, I stress ecological linkages. I do so because our historical local sphere of awareness still blinds us to the global ripples we cause today. Awareness lags far behind impact. Ecology cannot yet tell us the full consequences of our activity, deliberate or otherwise, but it can at least map its dimensions and alert us to plausible threats. I also stress biotic rather than abiotic processes, given the heavy emphasis on pollution, biogeochemical cycles, and climate change in environmental studies to date (13, 19). Following the ripples calls for new theories and tools and methods for detecting and predicting the outcome for ecosystems, planetary process, our own future, and ultimately the evolution of life on earth. Meanwhile, we must make informed guesses. I select a few of the larger stones we have cast into the ecosystem pond and, using evidence and theory, follow the ripples through a causal chain from impact on community structure to ecosystem process and function. I then follow one or two of the persistent ripples from ecosystem to biosphere to show how the backwash can affect species and communities locally.

I start with the most central issue in conservation biology today and the hallmark of human impact from genetic to landscape levels: the loss of biological diversity.

Diversity. What are the ecological consequences of reduced diversity? The evidence is inconclusive but tilts toward some predictable changes. So, for example, recent multisite studies across Europe show that productivity rises with species diversity (28, 29). The higher yields may arise from species complementary in resource use and perhaps positive species interactions (32). Whatever the cause, recent work points to the reverse phenomenon, a reduction in diversity leading to a loss of productivity (33). Diversity may also dampen variation in primary productivity during extreme stress such as droughts.

A great deal more experimental work is needed to clarify the relationships among diversity, food web structure and ecosystem properties (34, 35). Theoretical and experimental studies point to greater resistance to invasive species and pathogens as diversity increases (31, 36). Stability measured by return time (34) and compositional stability is not positively linked and may in fact be negative on theoretical grounds (37). Recent studies (38) show that external landscape factors and site history, rather than internal linkages, account for high stability in species-poor communities.

The difficulty of linking diversity and ecosystem properties probably tells us more about the inappropriateness of diversity as a generic measure than it does about human impact—or perhaps about the difficulty of drawing ecological generalities from the limited data so far available. Just as early debates over the link between diversity and stability floundered on the multitude of properties such as resilience, resistance, persistence, and variability (35), it is likely that we ask too much of diversity and miss the functional links between species composition and ecological process. The life history characteristics and the relative abundance of species is likely to tell us more about ecosystem change than species richness *per se* (39).

Functional Roles. Paine's (40) pioneering work on the role of the predatory starfish *Pilaster* in regulating species diversity in littoral communities was the first of many to highlight the role of keystone species in community structure and dynamics (41, 42). Recent work has broadened keystone species to functional groups. Functionally equivalent species contribute to keystone processes such as primary production by algal mats on coral reefs; here, individual species abundance may fluctuate, but the overall photosynthetic production remains relatively constant (43). It is quite possible that the maintenance of such functional groups is far more critical to the maintenance of ecosystem structure and properties than how many species are present, regardless of their role. Clarifying functional roles will help ecologists determine the ecological bottom line—those irreplaceable elements of ecosystems we cannot afford to lose.

The evidence already underscores the need to consider functional roles in tracing the ripple effect of human activity on ecosystem properties and points to a novel experimental tool for ecologists (44).

Structural Asymmetry. An obvious starting point is our differential impact on large species. The overharvesting of big species is our most ancient and persistent signature. Great Lakes fishery and New Brunswick forestry practices, for example, select large species because of their high price per unit mass. Overharvested species of trees and fish are further stressed by pesticides, acid rain, chemicals, and introduced species, causing a "general stress syndrome" (45). The outcome can be gauged from both theory and field studies. Size-scaling theory predicts such life history characters as growth rate, reproductive rate, intrinsic rate of natural increase, generation time, and turnover rate (39, 46). These life-history traits, derived from physiological scaling laws common to all plants and animals (47, 48), govern the demographic and population patterns for single species as well as their population cycle times and home ranges (39, 49). If community structure is the aggregation of species abundance, then ecosystem dynamics is the interactions of their relative abundance and life history traits—mediated by extrinsic environmental factors. So, for example, the size-frequency distribution of a species in an assemblage can be used to predict energy and nutrient turnover rates (39, 50). Scaling laws also explain packing rules that theoretically and empirically predict the relationship between diversity and productivity, and between species diversity and area (51).

Ecosystem Processes. By using life history theory, what can we infer about the ecological changes resulting from the extermination of large-bodied species? First, because large bodied species of predators and herbivores are keystone species, their extermination or reduction will further decrease species richness and habitat patchiness (26, 52). Second, the mean body size of species in a community will diminish. Third, population cycle times and overall community turnover rates will shorten. Fourth, nutrient flow rates will increase. Fifth, resilience will increase but resistance will decrease. Sixth, external agencies and stochastic events will increasingly govern community dynamics as the internal feedback linkages dominated by large animals weaken (53). Finally, the loss of important functional groups will also contribute to an overall loss in productivity.

The use of functional groups allows us test deductions about stability. We can deduce, for example, that resilience should decline with species succession—given the longer generation times of larger more competitive species—and, conversely, that resistance will decrease with species impoverishment because of a loss of niche specialization. We can also deduce that the loss of large mammals and their disturbance regimes will lead to further species loss and a weakening of internal stabilizing forces of herbivory, competition and predation.

Ecosystem Functions. I have used the example of asymmetrical impact of humans on species composition to trace the ripple effect of ecosystem structure and process. Whether such impacts show up in function is less clear (31). The causal linkage via size-structured communities suggests that nutrient cycles theoretically should be shortened and productivity lowered. Whether reflectance and water cycles are affected is also unclear. Large changes in biotic structure and process can occur without affecting ecosystem functions, and *vice versa*. So, for example, Schindler *et al.* (54) found in an experimental study of Canadian lakes that chemical perturbation causes large changes in species dominance, but that the functional properties of the ecosystem (productivity, water and nutrient cycles, reflectance) are unaffected. In contrast, sedentarization of livestock can change plant cover and reflectance through overgrazing in the absence of any increase in stocking levels. The mode of land use—the degree to which it mimics existing ecosystem properties—may, in other words, be more important than intensity.

I suspect that another problem clouding debate over the consequences of human impact biodiversity loss is the relatively small amounts of change ecologists study in natural systems. When it comes to the most extremely modified humanscapes—monocultures—the consequences of biodiversity loss are largely uncontested. Here, by almost any measure, ecosystem properties are profoundly simplified. Overall, diversity declines, the number of functional groups decreases, food chains are shortened and simplified, and resistance to invasive species and pathogens falls. Compositional stability alone may be higher, but only because of the ever-higher costs in terms of extrinsic energy and nutrients inputs.

So far I have focused on the direct impact of species removal on structure and internal ecosystem processes. The indirect and external effects are far greater for evolution. A few examples show the ripple effect of human impact in ecosystem, regional, and global processes.

Spatial Linkages. The unanticipated long-term consequences of fragmentation and loss of ecological linkages are only now becoming apparent. Dislocation of spatial links from ecosystem to continental level will see species extinctions progress up hierarchical scales starting locally in ecological time (decades to centuries) and extending into evolutionary time on a continental level (55). Fractal scales are important in resource partitioning and therefore in niche packing and diversity (51). Ecological gradients strongly partition niches and species in physical transition zones (56). Ecotones act as species refuges and speciation sites. Landscape fragmentation severs these spatial components vital to species diversity in space and time.

Spatial fragmentation also has a direct impact on individual species by snipping metapopulation connections, raising the risk of extinction through declines in species abundance, distribution, and interspecific interactions (57). The outcome is that smaller, less viable populations are vulnerable to stochastic processes such as disease, local environmental perturbations, genetic impoverishment, edge effects, and so on (58). Large species with low population densities and species with poor dispersal abilities across humanscapes are especially vulnerable to extinction.

Homogenization. Homogenization of ecosystems across the landscape reinforces the effects of fragmentation. The domestication of arable landscapes causes convergent ecosystem properties not only in species assemblage, but also in soil characteristics, nutrient and water cycles, and the dampening of stochastic events and perturbations. High nitrogen application on arable lands in moist climates and erosion-induced leaching in overgrazed arid lands are other example of large-scale homogenizing regimes. Based on Tilman's (59) resource ratio hypothesis, which predicts high species diversity at intermediate nitrogen levels, we might expect that species richness will diminish in both arable and arid lands.

Disturbance Regimes. Loss of disturbance regimes is yet another route to ecosystem simplification. The dampening of disturbance regimes, including sedentarization, can cause habitat simplification (52). Spatial fragmentation, homogenization, and loss of disturbance regimes collectively create secondary cycles of simplification within ecosystems as species diversity falls and internally driven processes maintaining species diversity weaken. The outcome favors small, easily dispersed species able to invade human-dominated ecosystems with low species diversity and resistance—the tramp species, colonizers, nitrogen-tolerant species, pests, and pathogens.

By-Products. At the risk of simplifying the vast literature on the environmental impact of pollutants, sediment and nutrient load, heat production, and so on, I use a few examples simply to show the overt consequences for ecosystems, the growing ripples globally, and the repercussions on communities and evolution.

The impact of pumping exogenous nutrients and energy into ecosystems and disposal of by-products of human activity are well established for nitrogen. Eutrophication of lakes and the oceans is showing up in algal blooms, loss of species, and lowered immune resistance (60). Fossil fuels emit sulfurous and nitrogenous compounds distributed by air currents and redeposited as acid rain, causing lake and forest impoverishment in industrialized countries (19). Fossil fuels also emit greenhouse gases that have raised atmospheric CO_2 levels, causing global warming, and are likely to alter climate on a time scale that matches the most violent shifts recorded in the last ten million years or more (13). Ecosystems everywhere could be affected by changes in temperature and rainfall in a matter of decades. Both the rapidity of climate change and the barriers to species dispersal (many of them anthropogenic) will challenge species adaptations and block migration, with grave implications for species extinction (61).

Table 3. Some ecological consequences of human activity on ecosystem processes

Ecosystem structure
Loss of biodiversity
Structural asymmetry and downsizing of communities
Loss of keystone species and functional groups
Ecosystem processes
Low internal regulation
High nutrient turnover
High resilience
Low resistance
Low variability
Low adaptability
Ecosystem functions
High porosity of nutrients and sediments
Loss of productivity
Loss of reflectance
Global processes
Modified biogeochemical cycles
Atmospheric change
Accelerated climatic change

The consensus on exogenous human impact is that every major planetary process, whether in biosphere, lithosphere, hydrosphere, or atmosphere, is already altered or dominated by our activity (12). Table 3 summarizes the main consequences of human activity on ecosystem properties.

The Evolutionary Implications

Human domestication of ecosystems greatly reduces species diversity. Of equal or greater importance, asymmetrical selective pressure on large species downsizes communities. Relatively small changes in keystone species and functional groups will have greater repercussions on ecosystem process than diversity as a whole. Downsized communities accelerate population, energy, and nutrient turnover rates, increase resilience, decrease resistance, and reduce overall productivity.

The dominant species—domesticated animals and plants—are heavily selected for specific traits and have reduced genetic heterogeneity and adaptability. Maintaining these traits and enhancing production in adverse environments and in the face of mounting disease and pathogen attacks will require ever-increasing energy inputs and environmental modification.

The expansion and intensification of domesticated landscapes will shrink habitats of nondomestic species, reduce population sizes, and fragment their range by imposing physical or biological barriers to dispersal. The resulting population declines and barriers select against poor dispersers, including big species. Small, easily dispersed species able to tap into the production cycle of domesticated landscapes and heavily harvested natural resources are selectively favored. These are typically r-selected weedy species and pathogenic and competitive microorganisms.

The selective pressures exerted by indirect human impact reinforce species extinctions and create deeper asymmetries and gaps in downsized communities. Three agencies of human activity reinforce these selective pressures:

(*i*) The secondary influence of fragmentation and homogenization of the landscape by reinforcing large-scale barriers at a regional and continental level. These large-scale barriers reduce periodic dispersal (due say to climate change) from continents to ecosystems and communities and vice versa, weakening the hierarchical links that maintain species richness (55).

(*ii*) The loss of disturbance regimes, either generated internally by keystone and functional species, or by external perturbations such as stochastic hydrological events.

(*iii*) The impact of human by-products such as heat, particulate matter, chemicals, and nutrients.

These three forces, among others, further amplify extinctions and asymmetries in community structure and favor small, high-dispersion species able to invade human-dominated ecosystems. The outcome will also accelerate speciation in small species able to survive fragmentary habitats in high enough densities to form viable founder populations and perhaps, ultimately, secondary specialization (62).

Finally, human activity will dominate biogeochemical cycles and affect major planetary processes such as climate through the greater porosity of energy flow and nutrients cycles across ecosystem boundaries and increased reflectance. One example is the impact of nitrogen overload on oceans through eutrophication and phytoplankton blooms (60) and their diminished resistance to invasive species (36).

There will, of course, be more that is unknown than known. By far the greatest uncertainty lies in predicting the scale and tempo of human land use changes. If these are slow, spatially homogenous, and persistent, species loss will be high. If the changes are local and transient, species may be able to disperse temporally and avoid mass extinction. The rate and scale of change in the mosaic of human land uses will have huge and as yet unpredictable consequences for evolution.

The Human Consequences

Assessing the implications for our own future is no simpler than it is for ecosystems. The future can be gauged from several points of view—from human carrying capacity, capacity for a given standard of living, or for the diversity of future options, for example (15). Should our horizon be measured in ecological or evolutionary time—in decades and centuries, or in millennia and millions of years? Cohen (17) has elegantly exposed the simplicity of Malthusian thinking in making projections over decades let alone centuries, given the sensitivity of the outcome to small changes in initial assumptions and the complex interactions involved in modeling human developmental scenarios.

One could well argue that our very success evolutionarily is proof of our ability to modify ecosystems to our advantage—and that we can take care of the environment in due course, when we can afford it. This is where the distinction between intentional modifications and side effects (Tables 1 and 2) becomes important. Kusnet's U-curve of wealth and environment, postulating that environmental clean-up follows wealth creation, has been development dogma for decades. There is now sufficient evidence to show that the Kusnet curve doesn't apply to fisheries and forestry in the developed world, let alone the poorer nations (63).

The challenge for ecology and environmental studies is to gauge the outcome of human action on ecosystem processes and on our own future. If there is no link between biodiversity and human well-being, then the future may be bleak for diversity but not necessarily for humanity. If that is the case, the fate of diversity will depend on human compassion, esthetics, and emotions rather than on human welfare.

Linking Ecological Impact and Human Welfare. Is there any link between biodiversity and human welfare? At best the connection is weak. Have we evidence to convince rural farmers that intensified monoculture is less productive and sustainable than biodiversity extraction? This is a dubious assertion, given the low limits on extractivism relative to intensive farming (64). Our intentional modification of food webs and landscapes is hard to fault based on evolutionary success to date. These modifications take on a different complexion, however, when the growing problems of overconsumption, ecological side effects, and rising costs are considered.

The cost of overconsumption can be measured in falling yields and rising costs. Nearly half of the world's marine fish populations are fully exploited and another 22% are overexploited (65). The real costs of food, resource, energy, and materials production are heavily disguised by massive subsidies, amounting to 1.5 trillion dollars globally each year (66). Stripped of subsidies, the costs of agriculture in the United Kingdom and perhaps many other developed countries already exceed the benefits (67). The mounting costs have been discounted in conventional gross domestic product measures, leading to calls for full-cost disclosure in valuing natural capital and ecological services (68). Removing these perverse subsidies would in itself improve economies and environment alike (66).

National governments share the academic's view of overconsumption to the point where environmental sustainability and security have risen to rise to top of the post-Cold War agenda. The Biodiversity Convention and a plethora of national biodiversity strategies testify to the consensus on the environmental threats of overconsumption and the need for sustainable practices (69).

We are on firmer ground yet when it comes to the side effects of our evolutionary strategies. A decline in environmental quality (measured by ecosystem process and function and build-up of deleterious waste products) does have a direct bearing on human health and well-being, as a few examples illustrate.

The rising health cost is the gravest concern because it does directly threaten our very survival, production, and reproduction—in short, our evolutionary success. Concerns over ozone thinning and increased UV levels, toxic pollutants, endocrine mimicking substances, immune suppression (70), and the spread of resistant and exotic infectious diseases including HIV, Ebola, and Marburg's virus are some examples (71).

Less important, but climbing the list of human concerns, is the quality of life. Urban living, the welter of human activity, and global travel will push the world tourism trade past the 4 trillion dollar mark in 2000. By 2020, some 20% of the global population is expected to take international trips (72). As awareness of environmental deterioration widens and appreciation of open space and more natural landscapes builds, the demand for quality of life will intensify. Environmental connections are being made where they matter most, in people's minds (14).

The Inadequate Response. The environmental connection could be construed as a turning point for conservation. It could further be argued that conservation is in place and showing success through protected area expansion, global agreements on greenhouse gases and ozone thinning, and perhaps even the plethora of national biodiversity strategies. Added to that is the good news of a worldwide demographic and economic transition and the improvement in numerous environmental indicators since the 1970s (19).

On the downside, these improvements come at a time when ecologists and conservationists alike realize that we have underestimated the magnitude of our environmental impact and the mitigation needs. Existing measures are far too paltry to save biodiversity or reverse environmental degradation. The global network of protected areas is too small to avert a rash of extinctions. Overharvesting of forests, fisheries, and wildlife continues unabated. Poverty and resource depletion is growing worse over much of the world, sapping the will and means to implement conservation measures.

How can conservation take hold under these conditions to avoid ecological homogenization, simplification, and degradation? How can we break past behavior patterns and change the projected course of evolution?

Applying Science to Conservation

The consequences of human impact, although largely unknown, are already troubling enough. The unknowns, no less than the immense amount of information needed to mitigate anticipated trends, pose the biggest of all challenges for science. Ayensu *et al.* (73), among others, have recognized the information gap in setting up an International Ecosystem Assessment (IEA) to conduct regular audits of human impact. The IEA is a fast-track solution to forecasting trends and integrating biological, physical, and socioeconomic studies for decision-making.

The need for information is growing critical. And yet, as Holling (49) points out, more information in itself is not the solution. Ecosystem models with ever more detail do not necessarily improve predictability. Arcane theories that fail to connect with reality are worthless. The Ecological Society of America (74) recognized the environmental and intellectual challenge in 1991 when it laid out an ecological research agenda for its Sustainable Biosphere Initiative. A decade later, some real progress has been made, but the challenge is more formidable than ever.

How can scientists keep up with such information demands? Perhaps a better way to phrase the question is: Given the catch-up problem, how can scientists provide better tools for environmental decision-making? Several interlinked steps are needed; I touch on them briefly.

Macroecological Theories. Ecological theory is essential in providing a robust, yet relatively simple explanation of ecosystems and their response to human activity. Community assembly rules and the relationship between ecosystem structure and process and how they vary biogeographically are basic to explaining overall diversity and ecosystem properties. In recent years, promising progress has been made on macroecological approaches (75–77). These nascent theories underscore the importance of scale and process in maintaining species diversity and ecological processes—and the links to continental scales (49, 55, 78).

Such models can help address question such as: Are there critical levels of diversity for a given ecological process? How much redundancy is there in ecological systems? What species or functional groups are vital to ecosystem structure and process? Can we use surrogate species to restore ecosystem properties? What critical thresholds exist for ecosystem properties in terms of species, processes, and area?

Ecological Principles. The maintenance of diversity, process, and function in ecosystems will depend on the identification of these critical properties and thresholds (49). Identifying threshold levels of tolerance provides the guidelines (or principles) on which sustainable development and conservation must be founded (79). Ultimately, simple principles are the basis of international agreements, conservation and development strategies, and management plans for all natural resources and biodiversity.

These questions only scratch the surface by touching on immediate threats and ecological time. Conservation biology has made a singular contribution by adding an evolutionary perspective to conservation (80). By identifying the selective forces of human impact and their consequences, ecologist are in a position to state principles for minimizing the evolutionary consequences of our action. I consider development of principles of sustainability that avoid evolutionary sclerosis to be the biggest task for ecologists. Table 4 illustrates some examples based on maintaining the ecosystem processes threatened by human activity (Table 3).

Table 4. Ecological principles for conserving ecosystem processes

Maintain or replicate
Species richness, structural symmetry, and keystone processes
Internal regulatory processes (e.g. predator–prey interactions)
External diversifying forces
Large habitat areas and spatial linkages between ecosystems
Ecological gradients and ecotones
Minimize
Erosion, nutrient leaching and pollution emissions
Landscape simplification
Landscape homogenization
Mimic
Natural process in production cycle

Methods. *In situ* restoration and *ex situ* management and tools and methods for improving data collection, monitoring and analyzing results, assessing risk, and defining minimum critical ecosystem parameters are vital for applying such principles to management (81). In recent years, cheap, accessible, high-resolution imagery has made large-scale environmental monitoring a reality. Techniques such as Population Viability Analysis and rapid techniques for biodiversity assessment have helped bridge the gap between time-consuming surveys and arbitrary judgments. Environmental Impact Assessments (EIA) and environmental monitoring have become prerequisites of development around the world in a remarkably short period. Further improvements in EIAs will depend on better ecological tools, methods, and application criteria.

Criteria. Finally, there is a dearth of criteria for identifying, safeguarding, or restoring biodiversity and ecological processes and gauging when and how to apply ameliorative measures (81). Such criteria help build consensus and develop a biological basis for conserving and managing biodiversity.

Until the last decade or so, ecological theory and conservation principles did no more than provide reactive short-term and small-scale solutions to ecological threats. Recent advances on both fronts offer better ways to determine sustainable harvests, set protected area priorities (82), and conserve entire ecological provinces through a minimum conservation area system nationally and regionally (83).

Applying Science and Conservation to Society

The Convention on Biological Diversity (CBD), adopted by over 120 nations, is the broadest conservation agreement ever reached. Its three goals—biodiversity, sustainable development, and equity—will guide global initiatives well into the 21st century. Achieving these goals will be difficult.

On the positive side, CBD shows high-level political commitment to the environment. Scientists have a central role to play in developing the ecological principles for CBD, national biodiversity strategies, EIAs, and sustainable development. On the negative side, the specialist nature of science and its aversion to the human-dominated landscapes distance it from society. Poor civic understanding of science echoes in conservation and the political arena. How can science-based conservation position itself to become a foundation for sustaining development and biodiversity in the 21st century? Ecologists have pointed out one flaw in our present strategies—inadequate concern with space and provision for the dynamical processes underlying biodiversity. Other challenges arise from changing society itself.

The Challenge of Change and Pluralism. The inherent weakness of conservation lies in big centralized government schemes (84) in the face of growing environmental threat and diminished treasury allocations. Governments simply cannot do everything everywhere by using the command-and-control method on which the modern movement was founded.

Societal change is also chipping away at the foundations of command-and-control conservation itself, particularly in the developing world. Here the spread of democracy in the post-Cold War era has raised awareness of rights and cultural identity. Pluralism in views and demands for equity in conservation benefits has intensified resistance to coercive conservation. The one-size-fits-all western conservation model is too doctrinaire today, ignoring cultural differences in philosophy, knowledge, society, and often what works already. Science is often seen as part of the top-down doctrine that disenfranchises local and rural communities, which bear the costs of conservation (85, 86).

These problems cut to the heart of CBD's goals of biodiversity, sustainable development, and equity. How can these goals be reconciled and implemented? How can they be achieved across human-dominated landscapes soon enough to maintain biodiversity and evolutionary adaptability? How can science-based conservation contribute more effectively to global and national development plans and local conservation efforts?

Balancing Local and Global Scales. The new conservation framework must address the hierarchical scales linking global and ecosystem processes by using mutually reinforcing top-down and bottom-up approaches (83). I touch briefly on both approaches to show the opportunity and need for science-based conservation.

Community-based conservation (CBC) has emerged over the last two decades in response to weakening governmental programs and new opportunities (85, 87). CBC is based on participation and emphasizes access rights, equity, and social responsibilities in conservation. It builds on local knowledge, skills, and institutions. Despite some success in watershed management, forestry, and wildlife conservation, CBC suffers from a lack of incentives, secular knowledge, self-organizing institutions, and local regulation.

In contrast, government efforts cover global conservation agreements, national policies, and strategic plans. These instruments set conservation principles, policies and strategies, legislation, incentives, and enforcement by using a variety of national institutions and public education. The transition from sectoral conservation (forestry, fisheries, wildlife, soil, water) to integrated landscape conservation and from centralization to devolved and interlinked efforts overseen by government will not be easy (84). Nongovernment agencies, universities, and the corporate world can help bridge top-down and bottom-up approaches, as shown in pluralism-by-the-rules negotiations on pollution abatement in the United States (88).

The role of science is central in developing the principles, criteria, methods, and overall accountability for sustainable development and biodiversity conservation linking top-down and bottom-up conservation approaches. However, creating spatially explicit linkages between institutions to match the scale of ecological and planetary processes calls for the best available information rather than exact science. How, then, can science be made applicable given the ignorance, uncertainty, urgency, lack of finance and human resources, social complexity, political realities, and cultural differences inherent to conservation?

Cultural perspective, local knowledge, and existing skills determine land use practice. Some practices are sustainable and compatible with conservation, others are not. The same can be said of ecological theories and conservation policies and practices.

Getting conservation going on a global and local scale in the face of these realities calls for rapid assessment techniques, setting up the basis for negotiation and partnerships, initiating a cycle of exchange, and procedures for reconciling science and local knowledge (83). We must make allowances for uncertainty and put in place adaptive management procedures to learn from successes and failures (89), whatever the source of knowledge or practice. How well we succeed will largely decide the outcome of future evolution.

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1. Gallagher, R. & Carpenter, B. (1997) *Science* **277,** 485.
2. Marsh, G. P. (1864) *Man and Nature; or Physical Geography as Modified by Human Action*; reprinted (1965) (Harvard Univ. Press, Cambridge, MA).
3. Golley, F. B. (1993) *A History of the Ecosystem Concept in Ecology* (Yale Univ. Press, New Haven, CT).
4. Tansley, A. G. (1935) *Ecology* **16,** 284–307.
5. Latour, B. (1999) *Pandora's Hope* (Harvard Univ. Press, Cambridge, MA).
6. Gould, S. J. (2000) *Science* **287,** 253–261.
7. Brundtland, G., ed. (1987) *Our Common Future* (Oxford Univ. Press, Oxford).
8. Carpenter, S. R., Chisholm, S. W., Krebs, C. J., Schindler, D. W. & Wright, R. F. (1995) *Science* **269,** 324–327.
9. Harris, D. R., ed. (1980) *Human Ecology in Savanna Environments* (Academic, London).
10. Martin, P. & Klein, R. G. (1984) *Quarternary Extinctions: A Prehistoric Revolution* (Univ. of Arizona Press, Tucson, AZ).
11. Martin, P. S. & Steadman, D. W. (1999) in *Extinctions in Near Time*, ed. MacPhee, R. D. E. (Plenum, New York), pp. 17–55.
12. Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. (1997) *Science* **277,** 494–499.
13. Hammond, A. (1998) *Which World? Scenarios for the 21st Century* (Earthscan, London).
14. Western, D. (1994) in *Natural Connections: Perspectives in Community-Based Conservation*, eds. Western, D., Wright, R. M. & Strum, S. (Island Press, Washington, DC), pp. 15–52.
15. Myers, N. (1987) *Conserv. Biol.* **1,** 14–21.
16. Jablonski, D. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5393–5398.
17. Cohen, J. E. (1995) *How Many People Can the World Support?* (Norton, New York).
18. Repetto, R., ed. (1985) *The Global Possible: Resources, Development and the New Century* (Yale Univ. Press, New Haven, CT).
19. Tolba, K., El-Kholy, O. A., El-Hinnawi, E., Holdgate, M. W., McMichael, D. F. & Munn, R. E., eds. (1992) *The World Environment 1972–1992, Two Decades of Challenge* (Chapman & Hall, London).
20. Heywood, V. H., ed. (1995) *Global Biodiversity Assessment* (United Nations Environmental Program, Cambridge, U.K.).
21. Clarke, W. C. & Munn, R. E., eds. (1986) *Sustainable Development of the Biosphere* (Cambridge Univ. Press, Cambridge, U.K.).
22. Primack, R. B. (1993) *Essentials of Conservation Biology* (Sinauer, Sunderland, MA).
23. McCormick, J. (1995) *The Global Environmental Movement* (Wiley, Chichester, U.K.).
24. Diamond, J. (1989) in *Conservation for the Twenty-first Century*, eds. Western, D. & Pearl, M. (Oxford Univ. Press, New York), pp. 37–41.
25. Patt, J. (1999) *What is Natural?: Coral Reef Crisis* (Oxford Univ. Press, New York).
26. Laws, R. M. (1970) *Oikos* **21,** 1–15.
27. Jewell, P. A. & Holt, S. (1981) *Problems in the Management of Locally Abundant Wild Mammals* (Academic, New York).
28. Western, D. (1989) in *Conservation for the Twenty-first Century*, eds. Western, D. & Pearl, M. (Oxford Univ. Press, New York), pp. 158–165.
29. Heerwagen, J. H. & Orians, G. H. (1993) in *The Biophilia Hypothesis*, eds. Kellert, S. M. & Wilson, E. O. (Shearwater, Washington, DC), pp. 138–172.
30. Kremer, M. (1993) *Q. J. Econ.* **108,** 681–716.
31. Chapin, S. F., Walker, B. H., Hobbs, R. J., Hooper, D. U., Lawton, J. H., Sala, O. E. & Tilman, D. (1997) *Science* **277,** 500–503.
32. Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., Finn, J. A., Freitas, H., Gillev, P. S., Good, J., *et al.* (1999) *Science* **286,** 123–127.
33. Tilman, D. (1999) *Science* **286,** 1099–1100.
34. Pimm, S. L. (1982) *Food Webs* (Chapman & Hall, London).
35. Pimm, S. L. (1992) *The Balance of Nature* (Univ. of Chicago Press, Chicago).
36. Stachowicz, J., Whitlatch, R. B. & Osman, R. W. (1999) *Science* **286,** 1577–1579.
37. May, R. M. (1973) *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, Princeton).
38. Sankaran, M. & McNaughton, S. J. (1999) *Nature (London)* **401,** 691–693.
39. Calder, W. A. (1984) *Size, Function and Life History* (Harvard Univ. Press, Cambridge, MA).

40. Paine, R. T. (1974) *Oecologia* **15,** 93–120.
41. Western, D. & Gichohi, H. (1993) *Afr. J. Ecol.* **31,** 268–281.
42. Crooks, K. R. & Soule, M. E. (1999) *Science* **269,** 316–317.
43. Stone, R. (1995) *Science* **269,** 316–317.
44. Roush, W. (1995) *Science* **269,** 313–315.
45. Rapport, D. J., Regier, H. A. & Thorpe, C. (1981) *Stress Effects on Natural Ecosystems* (Wiley, New York).
46. Western, D. (1979) *Afr. J. Ecol.* **17,** 184–205.
47. West, G. B., Brown, J. H. & Enquist, B. J. (1997) *Science* **276,** 122–126.
48. West, G. B., Brown, J. H. & Enquist, B. J. (1999) *Science* **284,** 1677–1679.
49. Holling, C. S. (1992) *Ecol. Monogr.* **62,** 447–502.
50. Western, D. (1983) *Oecologia* **59,** 269–271.
51. Ritchie, M. E. & Olff, H. (1999) *Science* **400,** 557–560.
52. Owen-Smith, N. (1989) *Conserv. Biol.* **3,** 405–412.
53. Roughgarden, J. (1986) in *Community Ecology*, eds. Diamond, J. & Case, T. J. (Harper and Row, New York), pp. 492–512.
54. Schindler, D. W. K., Daves, M. A., Turner, G. A. Lindsey, G. A. & Cruickshank, D. R. (1985) *Science* **228,** 1395–1401.
55. Rosensweig, M. L. (1995) *Species Diversity in Space and Time* (Cambridge Univ. Press, Cambridge, U.K.).
56. Silvertown, J., Dodd, M. E. & Gowing, D. J. E. (1999) *Nature (London)* **400,** 61–63.
57. Gonzalez, A., Lawton, J. H., Gilbert, F. S., Blackburn, T. M. & Evans-Freke, I. (1998) *Science* **281,** 2045–2047.
58. Soule, M. E., ed. (1987) *Viable Populations for Conservation* (Cambridge Univ. Press, Cambridge, U.K.).
59. Tilman, D. (1985) *Am. Nat.* **125,** 827–852.
60. Micheli, F. (1999) *Science* **285,** 1396–1398.
61. Root, T. L. & Schneider, S. H. (1995) *Science* **269,** 334–341.
62. Tilman, D. & Lehman, C. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5433–5440.
63. Ekins, P. (1999) *New Sci.* **2216,** 48–49.
64. Browder, J. O. (1991) *Bioscience* **41,** 286.
65. Botsford, L. W., Castilla, J. C. & Petersen, C. H. (1997) *Science* **277,** 509–515.
66. Myers, N. & Kent, J. (1998) *Perverse Subsidies* (International Institute for Sustainable Development, Canada).
67. Pearce, F. (1999) *New Sci.* **2217,** 10.
68. Dailey, G., ed. (1997) *Nature's Services: Societal Dependence on Natural Ecosystems* (Island Press, Washington, DC).
69. Hempel, L. C. (1996) *Environmental Governance* (Island Press, Washington, DC).
70. Chivian, E. (1997) in *Biodiversity and Human Health*, eds. Grifo, F. C. & Rosenthal, J. (Island Press, Washington, DC).
71. Daszak, P., Cunningham, A. A. & Hyatt, A. D. (2000) *Science* **287,** 443–449.
72. Bosselman, F. P., Peterson, C. A. & McCarthy, C. (1999) *Managing Tourism Growth* (Island Press, Washington, DC).
73. Ayensu, E., van Claasen, D. R., Collins, M., Dearing, A., Fresco, L., Gadgil, M., Gitay, H., Glaser, G., Juma, C., Krebs, J., *et al.* (1999) *Science* **286,** 685–686.
74. Lubchenco, J., Olson, A. M., Brubaker, L. B., Carpenter, S. R., Holland, M. M., Hubbell, S. P., Levin, S. A., MacMahon, J. A., Matson, P. A., Melillo, J. M., *et al.* (1991) *Ecol.* **72,** 371–412.
75. Rickleffs, R. E. (1987) *Science* **235,** 167–171.
76. Maurer, B. A. (1999) *Untangling Ecological Complexity* (Univ. of Chicago Press, Chicago).
77. Levins, S. (1999) *Fragile Dominion: Complexity and the Commons* (Helix, Reading, MA).
78. Pickett, S. T. A. & Cadenasso, M. L. (1995) *Science* **269,** 331–334.
79. Constanza, R., Andrade, F., Antunes, P., van den Belt, M., Boersma, D., Boesch, D. F., Catarino, F., Hanna, S., Limburg, K., Low, B., *et al.* (1998) *Science* **281,** 198–199.
80. Soulé, M. E. & Willcox, B. A., eds. (1980) *Conservation Biology: A New Evolutionary Perspective* (Sinauer, Sunderland, MA).
81. Western, D. (1992) *Oikos* **63,** 29–38.
82. Olsen, D. M. & Dinnerstein, E. (1998) *Conserv. Biol.* **12,** 501–515.
83. Western, D. (2000) *Issues Sci. Technol.* **16,** 53–60.
84. Scott, J. C. (1998) *Seeing Like a State: How Certain Schemes to Improve the Human Condition Have Failed* (Yale Univ. Press, New Haven, CT).
85. Furze, B., de Lacy, T. & Birckhead, J. (1996) *Culture, Conservation and Biodiversity* (Wiley, Chichester, U.K.).
86. Escobar, B. (1999) *Cult. Anthropol.* **40,** 1–30.
87. Warton, D. (1998) *Community and Sustainable Development* (Earthscan, London).
88. Weber, E. P. (1998) *Pluralism by the Rules: Conflict and Cooperation in Environmental Regulation* (Georgetown Univ. Press, Washington, DC).
89. Ludwig, R., Hilborn, R. & Walters, C. (1993) *Science* **260,** 17, 36.

Colloquium

The current biodiversity extinction event: Scenarios for mitigation and recovery

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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.

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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 antipollution 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.

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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).

Declines of biomes and biotas and the future of evolution

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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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Abbreviation: My, million years.

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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 attention (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.

I thank the numerous participants in the colloquium's formal and informal discussions. This essay constitutes my personal attempt, 8 months after the meeting, to highlight their contributions and concerns. Our discussions were unrecorded at the time; thus, errors and omissions are mine alone. I thank R. Lande, N. Myers, and K. Roy for improving the manuscript with their comments.

1. Myers, N. (1990) *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **82,** 175–185.
2. Myers, N. (1993) *Biodiversity Conserv.* **2,** 2–17.
3. Myers, N. (1996) *The Environmentalist* **16,** 37–47.
4. Costanza, R., d'Arge, R., deGroot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., *et al.* (1997) *Nature (London)* **387,** 253–260.
5. Pimentel, D. S., Wilson, C., McCullum, C., Huang, R., Dwen, P., Flack, J., Tran, Q., Saltman, T. & Cliff, B. (1997) *Bioscience* **47,** 747–757.
6. Cincotta, R. P. & Engelman, R. (2000) *Nature's Place: Human Population and the Future of Biological Diversity* (Population Action International, Washington, DC).
7. Vitousek, P. M., Mooney, H. A., Luchenco, J. & Melillo, J. M. (1997) *Science* **277,** 494–497.
8. Wilson, E. O. (1991) *The Diversity of Life* (Harvard Univ. Press, Cambridge, MA).
9. Hughes, J. B., Daily, G. C. & Ehrlich, P. R. (1997) *Science* **278,** 689–692.
10. Pimm, S. L., Russell, G. J., Gittleman, J. L. & Brooks, T. M. (1995) *Science* **269,** 347–350.
11. Purves, A., Agapow, P.-M., Gittleman, J. L. & Mace, G. M. (2000) *Science* **288,** 328–330.
12. Jackson, J. B. C. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5411–5418.
13. Graham, R. W., Lundelius, E. I., Graham, M. A., Schroeder, E. K., Toomey, R. S., Anderson, E., Barnosky, A. D., Burns, J. A., Churcher, C. S., Grayson, D. K., *et al.* (1996) *Science* **272,** 1601–1606.
14. Nee, S. & May, R. M. (1997) *Science* **278,** 692–694.
15. Main, A. R. (1982) in *Species at Risk. Research in Australia*, eds. Grove, R. H. & Ride, W. D. L. (Springer, Berlin), pp. 163–174.
16. Knowlton, N. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5419–5425.
17. Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., *et al.* (2000) *Science* **287,** 1770–1774.
18. Chapin, F. S., Sala, O. E. & Huber-Sanwald, E., eds. (2001) *Future Scenarios of Global Biodiversity* (Springer, New York), in press.
19. McKinney, M. L. & Lockwood, J. L. (1999) *Trends Ecol. Evol.* **14,** 450–453.
20. Lockwood, J. L. & McKinney, M. L., eds. (2000) *Biotic Homogenization* (Kluwer/Plenum, New York).
21. Louis Harris & Associates (1998) *Biodiversity in the Next Millennium Survey* (Am. Mus. Nat. Hist., New York).
22. Warrick, J. (1998) *Washington Post*, April 21, A-4.
23. Jablonski, D. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5393–5398.
24. Novacek, M. J. & Cleland, E. E. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5466–5470.
25. May, R. M., Lawton, J. H. & Stork, N. (1995) in *Extinction Rates*, eds. Lawton, J. H. & May, R. M. (Oxford Univ. Press, Oxford), pp. 1–24.
26. Alroy, J. (1999) *Syst. Biol.* **48,** 107–118.
27. Alroy, J. (1999) in *Extinctions in Near Time*, ed. MacPhee, R. D. E. (Kluwer/Plenum, New York), pp. 105–143.
28. Regan, H. M., Lupia, R., Drinnan, A. N. & Burgman, M. A. (2001) *Am. Nat.* **157,** 1–10.
29. Jablonski, D. (1995) in *Extinction Rates*, eds. Lawton, J. H. & May, R. M. (Oxford Univ. Press, Oxford), pp. 25–44.
30. Roy, K., Jablonski, D. & Valentine, J. W. (1996) *Philos. Trans. R. Soc. London B* **351,** 1605–1613.
31. Vitousek, P. M., D'Antonio, C. M., Loope, L. I. & Westbrooks, R. (1996) *Am. Sci.* **84,** 468–478.
32. Mooney, H. A. & Cleland, E. E. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5446–5451.
33. Ellstrand, N. C., Prentice, H. C. & Hancock, J. F. (1999) *Annu. Rev. Ecol. Syst.* **30,** 539–563.
34. Pimentel, D. S. & Raven, P. H. (2000) *Proc. Natl. Acad. Sci. USA* **97,** 8198–8199.
35. Roy, K., Valentine, J. W., Jablonski, D. & Kidwell, S. M. (1996) *TREE* **11,** 458–463.
36. Webb, T. & Bartlein, P. J. (1992) *Annu. Rev. Ecol. Syst.* **23,** 141–173.
37. Dynesius, M. & Jansson, R. (2000) *Proc. Natl. Acad. Sci. USA* **97,** 9115–9120.
38. Hewitt, G. (2000) *Nature (London)* **405,** 907–913.
39. Tilman, D. & Lehman, C. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5433–5440.
40. U.N. Population Division (1998) *World Population Projections to* 2150 (United Nations, New York).
41. Kirchner, J. W. & Weil, A. (2000) *Nature (London)* **404,** 177–180.
42. Erwin, D. H. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5399–5403.
43. Rosenzweig, M. L. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5404–5410.
44. Mayr, E. (1954) in *Evolution as a Process*, eds. Huxley, J., Hardy, A. C. & Ford, E. B. (Allen & Unwin, London), pp. 157–180.
45. Case, T. J. & Taper, M. L. (2000) *Am. Nat.* **155,** 583–605.
46. Templeton, A. R., Robertson, R. J., Brisson, J. & Strasburg, J. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5426–5432.
47. Wright, S. (1931) *Genetics* **31,** 39–59.
48. Young, A., Boyle, T. & Brown, T. (1996) *Trends Ecol. Evol.* **11,** 413–418.
49. Wilhelm, F. M. & Schlindler, D. W. (2000) *Funct. Ecol.* **14,** 413–422.

50. Lande, R. (1999) in *Genetics and the Extinction of Species*, eds. Landweber, L. F. & Dobson, A. P. (Princeton Univ. Press, Princeton), pp. 1–22.
51. Woodruff, D. S. (2001) in *Encyclopedia of Biodiversity*, ed. Levin, S. (Academic, San Diego), Vol. 4, pp. 811–829.
52. Srikwan, S. & Woodruff, D. S. (2000) in *Genetics, Demography, and Viability of Fragmented Populations*, eds. Young, A. & Clarke, G. (Cambridge Univ. Press, Cambridge, U.K.), pp. 149–172.
53. Frankel, O. H. & Soulé, M. E. (1981) *Conservation and Evolution* (Cambridge Univ. Press, Cambridge, U.K.).
54. Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W. & Hanski, I. (1998) *Nature (London)* **392,** 491–494.
55. Goodnight, C. J. (2000) *Proc. Natl. Acad. Sci. USA* **97,** 9365–9366.
56. Lande, R. (1995) *Conserv. Biol.* **9,** 782–791.
57. Chapin, F. S., Walker, B. H., Hobbs, R. J., Hooper, D. U., Lawton, J. H., Sala, O. E. & Tilman, D. (1997) *Science* **277,** 500–504.
58. Roy, K. & Foote, M. (1996) *Trends Ecol. Evol.* **12,** 277–281.
59. Janzen, D. H. (2001) in *Encyclopedia of Biodiversity*, ed. Levin, S. (Academic, San Diego), Vol. 3, pp. 689–699.
60. Barton, N. (2000) *Science* **290,** 462–463.
61. Avise, J. C. (2000) *Phylogeography* (Harvard Univ. Press, Cambridge, MA).
62. Schluter, D. (1998) in *Endless Forms: Species and Speciation*, eds. Howard, D. J. & Berlocher, S. H. (Oxford Univ. Press, Oxford), pp. 114–129.
63. Orr, M. R. & Smith, T. B. (1998) *Trends Ecol. Evol.* **13,** 502–506.
64. Knowles, L. L. (2000) *Evolution (Lawrence, Kans.)* **54,** 1337–1348.
65. May, R. M. (1988) *Science* **241,** 1441–1449.
66. Rapport, D. (2000) in *Ecosystem Health*, eds. Rapport, D., Costanza, R., Epstein, P. R., Gaudet, C. & Levins, R. (Blackwell, Oxford), pp. 3–17.
67. Myers, N. (1993) *Ambio* **22,** 74–79.
68. Wilson, E. O. (1994) *Naturalist* (Island Press, Washington, DC), p. 355.
69. Wilson, E. O. (2000) *Science* **289,** 2279.
70. Bisby, F. A. (2000) *Science* **289,** 2309–2312.
71. Edwards, J. L., Lane, M. A. & Nielsen, E. S. (2000) *Science* **289,** 2312–2314.
72. Woodruff, D. S. (1989) in *Conservation for the Twenty-First Century*, eds. Western, D. & Pearl, M. (Oxford Univ. Press, New York), pp. 76–88.
73. Crandall, K. A., Beinina-Emonds, O. R. P., Mace, G. M. & Wayne, R. K. (2000) *Trends Ecol. Evol.* **15,** 290–295.
74. Gould, S. J. (1982) *Science* **216,** 380–387.
75. Lande, R. & Shannon, S. (1996) *Evolution (Lawrence, Kans.)* **50,** 434–437.
76. Byers, D. L. & Waller, D. M. (1999) *Annu. Rev. Ecol. Syst.* **30,** 479–513.
77. Beaty, B. J. (2000) *Proc. Natl. Acad. Sci. USA* **97,** 10295–10297.
78. Olson, D. M. & Dinerstein, E. (1998) *Conserv. Biol.* **12,** 502–512.
79. Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. (2000) *Nature (London)* **403,** 853–858.
80. Pimm, S. L. & Raven, P. (2000) *Nature (London)* **403,** 843–845.
81. Mace, G. M., Balmford, A., Boitani, L., Cowlishaw, G., Dobson, A. P., Faith, D. P., Gaston, K. J., Humphries, C. J., Vane-Wright, R. I., Williams, P. H., *et al.* (2000) *Nature (London)* **405,** 393.
82. da Fonseca, G. A. B., Balmford, A., Bibby, C., Boitani, L., Corsi, F., Brooks, T., Gascon, C., Olivieri, S., Mittermeier, R. A., Burgess, N., *et al.* (2000) *Nature (London)* **405,** 393–394.
83. Western, D. (2000) *Issues Sci. Technol.* **16,** 53–60.
84. Western, D. (2001) *Proc. Natl. Acad. Sci. USA* **98,** 5458–5465.
85. Balmford, A., Mace, G. M. & Ginsberg, J. R. (1998) in *Conservation in a Changing World*, eds. Mace, G. M., Balmford, A. & Ginsberg, J. R. (Cambridge Univ. Press, Cambridge, U.K.), pp. 1–28.
86. Muller, H. J. (1949) in *Genetics, Paleontology, and Evolution,* eds. Jepsen, G. L., Mayr, E. & Simpson, G. G. (Princeton Univ. Press, Princeton), pp. 421–445.

Intervening in evolution: Ethics and actions

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Biologists should help to guide a process of cultural evolution in which society determines how much effort, if any, is ethically required to preserve options in biological evolution. Evolutionists, conservation biologists, and ecologists should be doing more research to determine actions that would best help to avoid foreclosing evolutionary options.

There is no question that *Homo sapiens,* in addition to causing the sixth major spasm of biotic extinction (1–4), is also altering the course of evolution for millions of years in the future. Many of the important issues raised by that alteration have been beautifully laid out by Norman Myers (5). Here I explore three overarching questions. The first is a fundamental background one: Where do ethics come from? This leads to the second. Considering that just two or three human generations are dramatically changing the biotas that will comprise a major portion of the environment of tens of thousands of future generations, what ethical obligations might this impose on scientists to respond in various ways? And the third is: If we are ethically obligated, what might scientists do to be more effective in informing society of its options in this area? These are complex issues; I deal only with the tip of the iceberg here.

The ethical questions about intervention in the evolutionary process are very similar to questions about the closely related issue of the preservation of biodiversity (2). Most of us believe that people in the future should be able to obtain from biodiversity a wide variety of esthetic pleasures, ecosystem goods, and, especially, ecosystem services (6). Humanity is now faced with the prospect of a continuing loss of the populations (7) and species (8) that supply those values. But, beyond this loss, society is taking actions that will modify both the rate of evolutionary regeneration of populations and species and the nature of the replacements produced. Our acceleration of the rate of extinctions and modification of the evolutionary process immediately raises an ethical issue long recognized by economists and others (9) as that of "intergenerational equity." The basic question is: At what rate, if any, is it moral for the current generation to discount the future? This question, in turn, leads us to the much more general questions of the origins and nature of ethical systems.

Where Do Ethics Come From?

Many people, following (most famously) Plato (10) and Kant (11), believe that, in essence, there exists a universe of ethics quite independent of the universe in which we dwell (or, equivalently, there is a god with all of the answers). To those holding that belief, answers to questions about the ethics of redirecting evolution have always been "out there"; our task is simply to discover them. Others believe that ethics can be derived directly from the evolutionary process itself—that, basically, whatever behavior has evolved is good because it evolved (for an overview, see ref. 12). They contend that one can determine what ought to be from what is (a contention that is often called by opponents of this view "the naturalistic fallacy"). I, and many others, take a third view (13): there is no extrinsic source of ethics, but human beings have evolved the capacity to hold and share values. Natural selection has, however, not helped us much in deciding what values to hold. The content of ethical systems—the things that a human being believes are right or wrong, moral or immoral—is assumed in this view to be almost entirely a product of cultural evolution.

Our dilemma of whether or how to change ethical systems so they can deal with human alteration of evolutionary processes assumes that cultural evolution is the primary source of values. After all, if there were an independent ethical universe we could tap into, it seems unlikely that ethics would differ as much as they do from culture to culture and time to time. A couple of centuries ago, slavery was ethically acceptable, as it had been since the dawn of history. It still is in some subcultures. An example, closer to the topic of this symposium, of cultural evolution that has altered ethics over the last few centuries is the widening of the circle of caring: the attribution of rights first to all human beings (as opposed to only some group of kin or pseudokin), then to domestic animals, then to charismatic wild animals, and eventually to all organisms and ecosystems. Furthermore, one can observe ethics evolving all of the time at a rate that cannot be explained by genetic evolution. It's happening at this meeting. No one was expressing concern about changing evolutionary trajectories even two decades ago. One could, of course, argue that the external ethical universe exists, and it is our communication with that universe or a deity that is continually culturally evolving. But that does not seem to be a very informative approach if we wish to understand the evolution of ethical systems. On the other hand, I see no sign that the process of evolution itself has provided many, if any, standards to undergird a system of ethics, including ethics about the maintenance of that process.

The evolution of ethics appears to be a product of a complex brain that evolved for, among other things, dealing with other smart individuals living in the same social groups. The roots of ethics seem to trace to the evolution of empathy—the ability to imagine another's viewpoint. Being able to consider the mental processes of members of one's group and relate emotionally to their states doubtless had a reproductive payoff and probably was a predisposition created by natural selection. But much of the behavior that "evolutionary psychologists" (e.g., refs. 14 and 15) and others attribute to genetic predispositions clearly can't be the direct result of biological evolution—we haven't the genes to do the job. Genes cannot incorporate enough instructions into the brain's structure to program an appropriate reaction to every conceivable behavioral situation, or even very large numbers of them. Here is an instance where a little bit of reductionist analysis suggests the hopelessness of seeking a genetic reductionist explanation of most of human behavior, including our ethical behavior related to the course of evolution (13). There are something on the order of 30,000 loci in the genome, whereas there are roughly 100 to 1000 trillion connections (synapses) between over a trillion nerve cells in our brains. That's at least

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one *billion* synapses per locus, even if every locus in the genome contributed to creating a synapse. Clearly, those connections can be only partially specified by genetic information; the environment and cultural evolution *must* play a very large, often dominant role in establishing the complex neural networks that modulate human behavior. To put it in shorthand, we could be said to have a "gene shortage," a point lost on popular writers in their enthusiasm to find "a gene" for every human behavioral characteristic (e.g., refs. 16 and 17).

Scientific Response to Human Modification of Evolutionary Trajectories

In this symposium, we are starting a dialogue over the ethical issues of human alteration of the future course of evolution, which can be viewed as an extension of the dialogue that already includes decision makers and the general public in discussions over human responsibility for abating the extinction crisis (18). I believe we can't look either to a deity or to evolution itself for answers. It is up to the human community to decide what the ethical course is, and to take whatever steps are then deemed ethically appropriate. Thus the answer to my second broad question seems to be that it is up to us as scientists to determine what are our own ethical obligations, and to help society at large to make its decisions.

Achieving some level of consensus on those obligations will not be an easy task. At one extreme, some will advise restoring huge areas of wilderness to provide evolutionary opportunities for continuation of megavertebrate diversification. That, clearly, is the view of those involved in the Wildlands Project (e.g., ref. 19)—and it's where I would come down emotionally if I could ignore the practical and ethical complexities of its implementation in most parts of the world. At the other extreme are the technological optimists who assume that genetic engineers will soon be able to produce any needed biodiversity to order and so see no reason to preserve what is left or worry about future evolutionary trajectories. They have a very high rate of discounting the future, because they assume that coming generations will be sufficiently richer and more technologically adept to solve any problems that altered evolution can present. This latter view will, of course, appeal to many in our gadget-oriented society, especially those who believe their financial security will be best protected under a "business as usual" scenario. And between those at the extremes (who will at least have considered the issue) will be the vast majority of humanity, people who simply see little reason to value most of biodiversity.

In the coming ethical debate, we must be extremely careful to take a broad view of the "human community" and not subconsciously assume that everyone shares the views of the community of evolutionary biologists, ecologists, and conservationists from rich countries. There is, understandably, considerable resentment in developing countries over what they view as a preference among conservation biologists for locking away land to protect biodiversity (and presumably future evolutionary options) without considering the present, sometimes dire needs of local communities or indeed of regions or even entire poor nations (20, 21). Choices will often have to be made between protecting the health and welfare of human beings living today, and risking those of future generations; evaluating such trade-offs and deciding on courses of action is likely to be difficult. For instance, revenue from logging a tropical forest might be used to help poor people living near the forest today. Would it be worth forgoing that revenue to preserve the forest as a potential generator of diversity that might improve the lives of people 2000 or 200,000 generations in the future? How are values to be assigned, and who should make this sort of decision? Is there any ethical need to consider the effects of today's actions that far or farther in the future? Could or should we strive to create such an ethical imperative? Can we possibly know enough to sensibly fashion an evolutionary ethic? Is it reasonable to imply an evolutionary discount rate of zero? Those who, like me, personally believe attention should be paid to the consequences of our actions for the long-term future must develop our arguments very carefully and not assume that there is a self-evident ethical need to do so.

Evolutionists, ecologists, and systematists can begin addressing these complex issues in four ways: through public education, interacting with those in other disciplines and walks of life, changing our research agendas, and working to find practical ways of influencing the evolution of ethics. Considering the long debate over the preservation of biodiversity (e.g., in the United States, continuing battles over the Endangered Species Act), it is clear to me that scientists concerned with answering the sorts of questions posed above and developing an ethics of preserving evolutionary processes will be caught in one of many mismatches in rates of cultural evolution (13). The speed at which society is changing the evolutionary prospect seems fated to remain much more rapid than the rate at which society is developing ethics to deal with the challenges that change may present. In this situation, the first and most obvious thing that we should do is alert the public and decision makers to the possible problem. I hope the colloquium on *The Future of Evolution* will mark the beginning of an effort by the concerned scientific community to do just that. Ecologists have gradually begun to realize that their responsibilities to society extend far beyond simply doing first-rate science and reporting the results in the scientific literature (22, 23). Evolutionists and systematists have lagged behind ecologists in awareness and action, but now is the time to start closing the gap (24).

Despite the uncertainties that are inherent in science, on issues of great importance to humanity, scientists must keep the public apprised of the latest consensus view of the pertinent scientific community (including recommendations for possible policy changes). Uncertainties, of course, should be made explicit in such communications, and when a scientist expresses a personal opinion diverging from the consensus, it should be clearly labeled as such. The idea that science should (or can) be value-free, a view expressed by several researchers recently (e.g., 23) and widely held in society, simply reflects a failure in the education of both scientists and members of the general public. The same can be said for the opinion that scientists should not make predictions about such things as future evolutionary trajectories because they may not be accurate, or the idea that one should wait until "uncertainties are resolved." Scientists, of course, make value judgments all of the time in their choice of projects (what is "worthwhile" investigating), choice of methods (e.g., how much disturbance of an ecosystem or injury to organisms would be justified by the information gained), and interpretation of results ("the most important conclusion from this study is . . ."). We cannot avoid such judgments, because being steeped in values is an important part of being human. The relative objectivity of science comes primarily not from the efforts we all make to be objective, but from adherence to rules (honesty, full disclosure of procedures, attempts to falsify one's own hypotheses), the adversarial nature of the enterprise (peer review, replication by others, eventual rewards for showing the paradigm has no clothes), and the existence of nature (an assumption) to serve as a final arbiter.

Making predictions is an important part of science, and a major challenge in the area of evolution is to make the best possible predictions on what human intervention means to the evolutionary process. We must seek ways that some of those predictions can be tested in the relatively short term. When the predictions are not fulfilled (they frequently will not be), the reasons for the failure should provide an entrée into finding just what part of the system was inadequately understood. And, of course, one thing that separates science from other ways of knowing is that uncertainties are never fully resolved. At best, the community agrees that the uncertainties are minimal (although many a paradigm has crashed after such agreement), and individual scientists will always differ on the degree of trust they put in a given conclusion. Our credibility should rest on the openness with which we explain the uncertainties, our readiness to change conclusions and recommendations as new data come in, being clear on how our own views relate to the scientific consensus, and persistence in telling politicians that neither they nor anyone else can supply absolute certainty on a scientific issue. Credibility cannot and should not rest on an implicit notion that "science" in the abstract can be trusted.

A second way that evolutionists, ecologists, and systematists can contribute fully to the cultural evolution of ethics relating to future biological evolution is to participate increasingly in interdisciplinary research and interaction with people with different backgrounds and attitudes. We will wish to outline for society the likely consequences of alternative courses of action (or inaction) and, at least by implication, advocate certain courses of action. But without input from economists, political scientists, legal scholars, the business community, and others, some of the alternatives presented may at best have little chance of acceptance by society as a whole, or at worst produce results counter to those intended. Remember, it is not for us to dictate what society wants, but rather to interact vigorously with the public in an attempt to achieve ends that both make sense scientifically and are socially and politically feasible. As I indicated, in virtually all cases, society will be faced with increasingly difficult choices among alternate courses of action. Many will involve trade-offs between desirable outcomes, and scientists must help to clarify them. As individuals, not as scientists, we also may advocate our own preferences. The latter is important; although we cannot dictate a course of action to the rest of society, neither should we be disenfranchised when it comes to social decision making.

Third, beyond improving scientific outreach, we should be reexamining our research agendas so that they yield as much information as possible pertinent to evaluating the scale of anthropogenic impacts on the future course of biotic evolution, and attempting to find ways to ameliorate those considered potentially the most serious—as Norman Myers has been urging for more than a decade. The papers presented in this colloquium indicate that this process is finally underway, and much recent work is, perhaps serendipitously, pertinent to major issues. For instance, the question of whether isolation is the key to geographic speciation (25–27) or whether differences in selection pressures are equally or more important (28) is now being reexamined in some detail (29). The answer to that question could be important if society decides that it wishes to encourage the continued generation of diversity. If different selection pressures are paramount, then the unplanned trend toward reducing once-continuous tracts of habitat into many isolated but similar fragments will not enhance speciation to the degree that some may hope. In any case, we don't know enough to establish with confidence conservation priorities aimed to influence future evolutionary effects.

One example of a potentially fruitful research agenda is that of the new discipline of countryside biogeography (30–32). Ecologists and conservation biologists have recently started to realize that there is no longer such a thing as an undisturbed habitat—no pristine systems to study. They have begun to focus more attention on the ecology of organisms in the vast areas that have already experienced substantial anthropogenic disturbance. The goals of countryside biogeography include determining what elements of biodiversity are best able to persist in altered habitats, establishing the relationship between degree of intensification of land use and an area's conservation value, evaluating the importance of remnant habitat to the delivery of ecosystem services, and finding ways to enhance the conservation/service-delivery value of human-dominated countrysides. This work could also provide a foundation for what we might call "countryside evolution," which could examine the possible impact of various patterns of habitat alteration on evolutionary trajectories and seek ways to enhance the evolutionary potential of communities persisting in areas heavily impacted by human activities.

It is clear that the activities of *Homo sapiens* are dramatically altering the future course of biological evolution, and, if current trends continue, the degree of alteration is likely to accelerate and lead to substantial discontinuities. But the possible consequences of this for humanity are much less obvious, so it is hard to present specific options except self-evident ones such as: "if society wishes to preserve opportunities for continued diversification of large animals in groups such as the big cats, horses, antelopes, and our closest primate relatives, more effort should be put into the conservation of large tracts of wilderness." More broadly—and more importantly—environmental scientists today can simply recommend that those whose values include a concern for the options of distant future generations take more care when meddling in a process billions of years old, which, when severely perturbed, could change the biosphere dramatically for millions of years in unpredictable ways. We can and should do better.

Fourth, in addition to adding to the knowledge base that society will need in its decision-making, scientists should participate in the hard work of outlining feasible ways of accomplishing changes they deem advisable. Although the mismatch—between the rate at which society is altering the evolutionary future and the rate at which it is recognizing, evaluating, and taking action on the issue—is severe, we should not despair. The rate at which our society evolves new ethics to deal with various aspects of the human predicament, including the evolutionary dilemma, can be accelerated. Cultural evolution clearly can be directed (13, 33), but a determined effort by a large and diverse sample of people is required. This symposium must be just a beginning.

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1. Myers, N. (1979) *The Sinking Ark* (Pergamon, New York).
2. Ehrlich, P. R. & Ehrlich, A. H. (1981) *Extinction: The Causes and Consequences of the Disappearance of Species* (Random House, New York).
3. Sepkoski, J. J., Jr. (1986) in *Patterns and Processes in the History of Life*, eds. Raup, D. M. & Jablonski, D. (Springer, Berlin), pp. 277–295.
4. Leakey, R. & Lewin, R. (1995) *The Sixth Extinction: Patterns of Life and the Future of Humankind* (Doubleday, New York).
5. Myers, N. (1996) *Environmentalist* **16,** 37–47.
6. Daily, G. C. (1997) *Nature's Services* (Island Press, Washington, DC).
7. Hughes, J. B., Daily, G. C. & Ehrlich, P. R. (1997) *Science* **278,** 689–692.
8. Wilson, E. O. (1992) *The Diversity of Life* (Harvard Univ. Press, Cambridge, MA).
9. Costanza, R. (1991) *Ecological Economics: The Science and Management of sustainability* (Columbia Univ. Press, New York).
10. Honderich, T. (1995) *The Oxford Companion to Philosophy* (Oxford Univ. Press, Oxford), pp. 683–686.
11. Kant, I. *The Metaphysics of Morals*, trans. Mary Gregor (1996) (Cambridge Univ. Press, Cambridge, U.K.).
12. Nitecki, M. H. & Nitecki, D. V. (1993) *Evolutionary Ethics* (State Univ. of New York Press, Albany, NY).
13. Ehrlich, P. R. (2000) *Human Natures: Genes, Cultures, and the Human Prospect* (Island Press, Washington, DC).
14. Barkow, J. H., Cosmides, L. & Tooby, J. (1992) *The Adapted Mind: Evolutionary Psychology and the Generation of Culture* (Oxford Univ. Press, New York).
15. Geary, D. C. (2000) *Psychol. Bull.* **126,** 55–57.
16. Hamer, D. & Copeland, P. (1998) *Living with Our Genes: Why They Matter More Than You Think* (Doubleday, New York).

17. Ridley, M. (1999) *Genome: The Autobiography of a Species in Twenty-Three Chapters* (HarperCollins, New York).
18. Soulé, M. E. & Lease, G. (1995), *Reinventing Nautre: Responses to Postmodern Destruction* (Island Press, Washington, DC).
19. Soulé, M. E. (1999) *Wildlands* **9,** 38–46.
20. Guha, R. (1989) *Environ. Ethics* **11,** 71–83.
21. Guha, R. (1997) *Ecologist* **27,** 14–21.
22. Bazzaz, F., Ceballos, G., Davis, M., Dirzo, R., Ehrlich, P. R., Eisner, T., Levin, S., Lawton, J. H., Lubchenco, J., Matson, P. A., *et al.* (1998) *Science* **282,** 879 (lett.).
23. Kaiser, J. (2000) *Science* **287,** 1188–1192.
24. Ehrlich, P. R. (1997) *A World of Wounds: Ecologists and the Human Dilemma* (Ecology Institute, Oldendorf/Luhe, Germany).
25. MacArthur, R. H. & MacArthur, J. W. (1961) *Ecology* **42,** 594–598.
26. Mayr, E. (1942) *Systematics and the Origin of Species* (Columbia Univ. Press, New York).
27. Mayr, E. (1963) *Animal Species and Evolution* (Harvard Univ. Press, Cambridge, MA).
28. Ehrlich, P. R. & Raven, P. H. (1969) *Science* **65,** 1228–1232.
29. Brown, K. (1999) *New Sci.* **20,** 46–49.
30. Daily, G. C. (2000) in *Nature and Human Society: The Quest for a Sustainable World,* ed. Raven, P. H. (Natl. Acad. Press, Washington, DC).
31. Daily, G. C., Ehrlich, P. R. & Sanchez-Azofeifa, A. (2001) *Ecol. Appl.* **1,** 1–13.
32. Ricketts, T., Daily, G. C., Ehrlich, P. R. & Fay, J. P. (2001) *Conserv. Biol.*, in press.
33. Ornstein, R. & Ehrlich, P. (1989) *New World/New Mind: Moving Toward Conscious Evolution* (Doubleday, New York).

National Academy of Sciences Colloquium

The Future of Evolution

March 16–19, 2000

Program

Friday, March 17, 2000

Session I

Norman Myers, Oxford University, and Andrew Knoll, Harvard University
Introduction

David Jablonski, University of Chicago
Lessons from the Past: Evolutionary Impacts of Mass Extinctions

Doug Erwin, National Museum of Natural History, Smithsonian Institution
Lessons from the Past: Biotic Recovery from Mass Extinctions

Alan Templeton, Washington University, St. Louis
Disrupting Evolutionary Processes

Michael Gilpin, University of California, San Diego
Metapopulation Dynamics

David Western, Wildlife Conservation Society and African Conservation Centre
Ecosystem Survival in a Human-Dominated World

Session II

Mike Rosenzweig, University of Arizona
Speciation: Past, Present, and Future

Nancy Knowlton, University of California, San Diego
Reef Ecosystems of the Future

Jeremy Jackson, University of California, San Diego
Biodiversity Decline in the Marine Realm

Fakhri Bazzaz, Harvard University
Plant Biology of the Future

Richard Cowling, University of Cape Town
Rapid Plant Diversification: Planning for an Evolutionary Future

Hal Mooney, Stanford University
Alien Invasions and Mixing of Biotas

David Tilman, University of Minnesota
The Vacant Niches of Human-Dominated Ecosystems

Paul Ehrlich, Stanford University
Intervening in Evolution: Ethics and Actions

Saturday, March 18, 2000

Session III

Discussion Leader, Peter Kareiva, University of Washington
Panel I: Ecological Modeling of Current and Future Diversity Threats

Discussion Leader, Russ Graham, Denver Museum of Natural History
Panel II: Lessons from the Pleistocene

Discussion Leader, David Woodruff, University of California, San Diego
Panel III: Decline of Biomes and Biotas

Discussion Leader, Michael Novacek, American Museum of Natural History
Panel IV: Scenarios for Recovery

Sunday, March 19, 2000

Session IV

Panel Reports

Session V

Conclusions