

There is a false paradox about conservation programs and time scale. A critic might ask, "Why the haste if conservation projects must last centuries?" The problem is that the current rate of biotic destruction demands immediate actions. This is not inconsistent with the objective that they persist a long time.

38. R. Repetto, Ed., *The Global Possible: Resources, Development, and the New Century* (Yale Univ. Press, New Haven, 1985); H. E. Daly and J. C. Cobb, Jr., *For the Common Good: Redirecting the Economy Toward Community, the Environment, and a Sustainable Future* (Beacon, Boston, 1989).
39. P. M. Vitousek, P. R. Ehrlich, A. H. Ehrlich, P. A. Matson, *BioScience* **36**, 368 (1986).
40. P. Ehrlich and E. O. Wilson, *Science* **253**, 758 (1991).
41. R. Ornstein and P. R. Ehrlich, *New World, New Mind* (Doubleday, New York, 1989).
42. B. Devall and G. Sessions, *Deep Ecology* (Gibbs M. Smith, Layton, UT 1985); A. Leopold, *A Sand County Almanac and Searches Here and There* (Oxford Univ. Press, Oxford, 1948); *World Conservation Strategy: Living Resources Conserved for Sustainable Development* (International Union for the Conservation of Nature, Nairobi, Kenya, 1980).
43. D. Ehrenfeld, *The Arrogance of Humanism* (Oxford Univ. Press, New York, 1981); C. Birch and J. C. Cobb, Jr., *The Liberation of Life: From Cell to the Community* (Cambridge Univ. Press, Cambridge, 1986).
44. P. S. Martin and R. G. Klein, Eds., *Quaternary Extinctions: A Prehistoric Revolution* (Univ. of Arizona Press, Tucson, 1984); S. T. Olson, in *Conservation for the Twenty-first Century*, D. Western and M. C. Pearl, Eds. (Oxford Univ. Press, New York, 1989), pp. 50–53.
45. P. M. Chandler, *Agriculture and Human Values* **8**, 59 (1991); T. H. McGovern, G. Bigelow, T. Amorosi, D. Russell, *Human Ecology* **16**, 225 (1988).
46. R. B. Norgaard, in *Biodiversity*, E. O. Wilson and F. M. Peter, Eds. (National Academy Press, Washington, DC, 1988), pp. 206–211.
47. D. E. Goodman and W. H. Friedland, personal communication.
48. P. H. Raven, in (22), pp. 119–122; M. J. Plotkin, in *ibid.*, pp. 106–118.
49. S. Postel in *State of the World* (Norton, New York, 1989), pp. 21–40.
50. For example, S. Hecht and A. Cockburn, *The Fate of the Forest: Developers, Destroyers and Defenders of the Amazon* (Harper Perennial, New York, 1990); to this extent, the working principle of some international conservation organizations that economic development is a necessary, let alone sufficient, precondition for conservation is untested.
51. H. H. Iltis, *Environment* **25**, 55 (1983).
52. G. E. Machlis and D. L. Tichnell [*The State of the World's Parks* (Westview, Boulder, CO, 1985)] report that 95% of tropical reserves report poaching of wildlife.
53. For example, F. Kajanja and I. Douglas-Hamilton, in *National Parks, Conservation and Development: The Role of Protected Areas in Sustaining Societies*, J. A. McNeely and K. R. Miller, Eds. (Smithsonian Institution Press, Washington, DC, 1984), pp. 80–86.
54. The Biosphere Reserve concept of Unesco's Man and the Biosphere Program is, in

part, an attempt to integrate economic development and conservation by sharing the management and benefits of protected areas with local peoples. It attempts to avoid the extremes of banishing people to save nature and banishing nature for the sake of people. It has been difficult to apply in practice [see D. Hales, in (4), pp. 139–144]; M. Batisse, *Nat. Resour.* **22**, 1 (1986); S. R. Kellert, *Environ. Conserv.* **13**, 101 (1986).

55. U. S. Seal, in *Endangered Birds: Management Techniques for Preservation of Threatened Species*, S. A. Temple, Ed. (Univ. of Wisconsin Press, Madison, WI, 1978), pp. 303–314; W. D. Newmark, *Nature* **325**, 430 (1987); P. F. Brussard, *Ecol. Appl.* **1**, 6 (1991); R. L. Peters and J. D. Darling, *BioScience* **35**, 707 (1985).
56. L. Silberling, *BioScience* **41**, 284 (1991); J. R. Browder, *ibid.* **40**, 626 (1991); J. R. Browder, *ibid.* **41**, 286 (1991).
57. An example is North American ranches harboring African ungulates. Entrepreneurs might consider the purchase of strategically located islands and other real estate where secure facilities could be located. See also M. E. Soulé, in *Conservation of Threatened Natural Habitats*, A. V. Hall, Ed. (South African National Science Programmes Report 92, CSIR Foundation for Research Development, P.O. Box 395, Pretoria, South Africa), pp. 46–65; M. E. Soulé, in (4), pp. 297–303.
58. M. E. Soulé, *Conserv. Biol.* **4**, 233 (1990).
59. M. A. Altieri and L. C. Merrick, in (22), pp. 361–369.
60. Although the vast majority of native species currently are unable to survive in intensively managed agricultural zones, especially in the tropics, sound agroecological practices create a healthy environment and contribute to self-sufficiency and the maintenance of crop genetic resources, especially if practiced in an economically and political stable environment. In addition, they may effectively reduce wood-collecting, hunting, and other pressures on nearby wildlands [see M. A. Altieri and D. K. Letourneau, *Crop Protect.* **1**, 405 (1982); S. R. Gliessman, E. R. Garcia, A. M. Amador, *Agro-Ecosystems* **7**, 173 (1982)].
61. Among the most recent and impressive acquisitions by The Nature Conservancy is the purchase in 1990 of the 130,000-ha Gray Ranch in southwestern New Mexico, which includes an entire mountain range (Las Animas).
62. J. M. Scott, B. Csuti, K. Smith, J. E. Estes, S. Caicco, in (1), pp. 282–297. See also Part IV of (1).
63. See L. A. Greenwalt, in (1), pp. 31–36; M. J. Bean, in *ibid.*, pp. 37–42; D. D. Murphy, in *ibid.*, pp. 181–198.
64. R. Reed, *Nat. Areas J.* **7**, 2 (1987); L. D. Harris and J. Eisenberg, in (4), pp. 166–181.
65. D. Western, in (4), pp. 158–165.
66. Others have called for greater respect for pluralism [D. Western, in (4), pp. vi–xv; R. F. Noss, in (1), pp. 227–246].
67. *Giving and Volunteering in the United States: Summary of Findings* (Independent Sector, 1828 L Street, NW, Washington, DC, 1988).
68. The manuscript was much improved thanks to the comments of D. B. Botkin, P. R. Ehrlich, D. Goodman, W. P. Gregg, Jr., R. E. Grumbine, D. F. Hales, J. A. McNeely, P. Romans, J. M. Scott, D. Wilcove, and G. Zegers.

An Evolutionary Basis for Conservation Strategies

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CONSERVATION STRATEGIES HAVE BEEN REMARKABLY ANTHROPOCENTRIC from their inception in the Middle Ages to the present (1, 2). During dynastic and feudal times, parts of kingdoms were set aside as hunting grounds for the aristocracy, thus preserving everything that dwelled therein. This, plus severe natural and cultural control of human populations resulted in environmental protection for centuries. Today, with a burgeoning and expanding human population of 5.3 billion, no more than 4500 areas are protected globally (1); that is equivalent to a mere 3.2% of our planet's landmass. National parks, wildlife refuges, biosphere reserves, military reserves, Indian reservations, and other forms of legally protected areas have been established for aesthetic, political, or practical purposes in the last 150 years. Many reserves in less-developed nations are paper parks only; many in the more developed are lamentably endangered by touristic herds, and certain wilderness parks are threatened by short-sighted national energy policies.

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Today, conservation strategy is based on a perceived impending loss of biodiversity due to tropical deforestation or disappearing habitats where populations of "interesting" species, subspecies, or even varieties (especially in temperate areas) reside. Campaigns usually focus on loss of potentially useful resources, such as plants with pharmaceutical properties or large animals that capture human interest. In practice, this results in saving fauna and flora in a few "available" acres where a well-known target taxon lives. Science has been too slow in providing inventory data to do much more; thus, what should be a major collective effort between conservation and science is often nonexistent, or in some cases, discord.

In the past 3 billion years, more species and their natural assemblies with their particular interactions have come and gone than are now present on Earth (3). One fact of evolution is that species go extinct, and others come into existence. Today, because of unprecedented human impact, species are increasingly going extinct and the speciation process, which creates future biodiversity, is being severely pressured through the removal of contiguous related biotic habitats. The pattern of continental habitats, often vast biomes, is being reduced to one of scattered island-like habitats and, just as on real islands, major extinctions are destined to occur. If this disruption of natural systems continues into the 21st century, we can expect the evolutionary process as we know it to become degraded and retarded.

There is no unified scientific method behind conservation strategy that addresses the nature and quantity of biodiversity, nor what it means environmentally either to save it or lose it outside direct

human interest. In fact, there is little altruism or science in the fight to save the rain forest, the spotted owl, or the Antioch blue butterfly. Rather, politics and economics weigh heavily on most decisions. It seems that degradation and conversion of the environment is proceeding so rapidly that getting something preserved—anything at all—is acceptable regardless of the yardstick. Worst of all is that legitimate arguments within the scientific and conservation communities allow decision-makers an out in politically difficult choices. In order to supplement positive conservation practices and provide an alternative to negative ones, an effort to establish a sound scientific underpinning must be made. Scientific rationale may transcend cultural changes through time, whereas economic and political grounds certainly will not.

What is biodiversity? Is it important, and if so, important to what? Is it possible to separate contemporary human needs from what is really necessary for the long-term environmental health of the planet? How can we hope to manage 30 or more million species? Given the myriad of societal demands and an ever-increasing population, what can realistically be achieved even if a global effort is sustained in environmental management? Should conservation strategy be scientifically or culturally based? These and others are the tough questions with which political systems must deal. For scientists, the question is what can we provide from our science that will help generate a long-term, transcultural foundation on which conservation strategy can be based?

Biodiversity can be equated with species richness, that is the number of species, plus the richness of activity each species undergoes during its existence through events in the life of its members, plus the nonphenotypic expression of its genome. Biodiversity evolves through numerous processes that vary from locality to locality, habitat to habitat. Species richness at a site is a readily observable index of the number of interactions among and between species and how these species are grouped as a living unit at that site. A species richness index then is a reasonable and knowable tool that can be used in setting policy and making decisions about biotic conservation and management. To understand the significance of a biodiversity index across geography, one needs context. Relationships between species and a knowledge of lineages to

which they belong provide that context.

Radiation of lineages of organisms occurring on both continents and islands proceeds stepwise and requires contiguous habitats of various kinds through which sequences of phylogenetically related species pass as the lineage to which they belong rises to dominance (within the context of the occupied habitat) and ebbs to extinction (4, 5). Centers of endemism, or relict occurrences of organisms, are the last remaining footholds of past radiations. Elsewhere these endemic organisms have been replaced by better adapted lineages to an ever-changing contemporary environment. This model taken to its extreme, given current trends, indicates that within a few hundred years this planet will have little more than lineages of domestic weeds, flies, cockroaches, and starlings, evolving to fill a converted and mostly desertified environment left in the wake of nonenvironmentally adaptive human cultural evolution.

What should we know to aid in countering the planet's impending biotic destruction? Assuming that it is the species radiation part of the evolutionary process, the generator of biodiversity, which is endangered, and that is what we (altruistically) decide to protect through scientifically based choices rather than cultural ones, we need to know where lineages (not individual species) originate innovations in their evolution and how these become distributed over some part of the planet. The disciplines involved to achieve this are phylogenetics and biogeography, together referred to as systematics. We need to use this science to tell us where the critical areas are that need sound environmental management—that is, where we need to protect the active processes of contemporary evolution. The most powerful tool to emerge during the past 20 years as a robust and comparative science, with both practitioners and theoreticians, is phylogenetics (6, 7) and its methods and applications (8, 9). Phylogenetics is well suited to provide predictions of as yet unobserved qualities that are directly applicable to conservation decision-making (10) and because its tools are now computer-based it can be applied in a short time to many groups for detecting congruence in patterns of occurrence of radiating lineages (9). Site congruence, which can be mapped easily, of many evolving lineages can then become the target of conservation activities.

A cladogram illustrating the hypothetical phylogenetic relationships among seven known species that make up a monophyletic lineage of organisms is shown in Fig. 1. According to such an analysis, species A and B have not demonstrated radiation—that is, the ability to evolve into a more broadly adaptive and widespread lineage through time. Both are found to be geographically restricted endemic forms (relicts) occupying small areas. Current conservation strategy places highest priority for protection on such areas as 1 and 2 (11). Endemic forms such as A and B are often unusual or rare, and even interesting to many scientists (12), but they are predictably on their way to extinction. These forms carry information about past evolutionary flourishes; they are important to protect, but they are only half the picture. The relatively more recent phylogenetic radiation and dynamic changes in taxa are occurring today and will occur in the future. Species such as C, D, E, and F are sometimes widespread and may even be regarded as “weedy” species, but does that make them less important? Their stem has become the multi-species sublineage that holds the most promise for continued evolution of this line of biodiversity under natural conditions. For example, in the *eucera* sublineage of the carabid beetle genus *Agra* (9) (Fig. 2), current interest would focus on areas D and F, each of which contains a relatively primitive and rare species. The cladogram (Fig. 2) shows that areas B and E contain both recent radiation and older species of the sublineage. If the *eucera* sublineage were something of general conservation interest, then the investment for protection would be better put into areas B and E to maximize

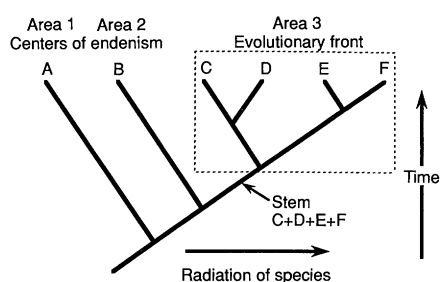


Fig. 1. Simple cladogram of seven species in a monophyletic lineage. More complex lineages may have more than one evolutionary front.

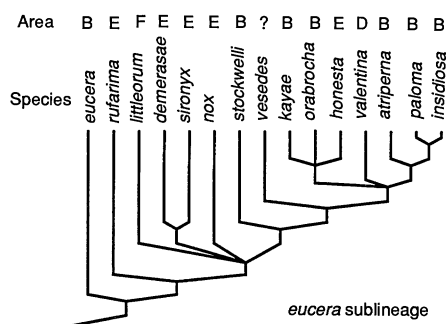


Fig. 2. Cladogram of the *eucera* sublineage of the carabid beetle genus *Agra* (9).

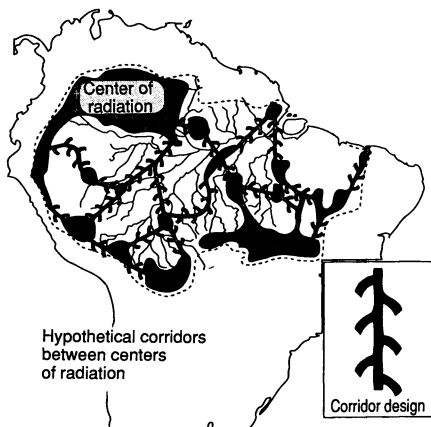


Fig. 3. Future corridors of ecological reconstruction between hypothetical centers of radiation—for example, in the Amazon Basin, to allow species movements and radiation. Inset is a design for a corridor that maximizes soil and habitat types in small areas.

salvaging this kind of beetle diversity now and in the future. Vane-Wright *et al.* (13) provide a novel index for cladogram analysis that needs careful testing in its application to making choices in conservation of taxic diversity. Congruence across many groups with their method may be the best way to find centers of radiation for conservation purposes.

Conservation strategy should incorporate methods to detect such contemporary evolution for the good of future maximum biodiversity. Conservation of only an accumulation of mostly nonradiating endemic taxa, the current conservation strategy (11), is like saving living fossils, something of human interest, but perhaps not beneficial to the protection of evolutionary processes and environmental systems that will generate future biodiversity.

Through analyses of diverse groups and detection of congruent patterns among radiating lineages (8), evolutionary fronts (centers of radiation) can be detected and targeted for long-term protection. Site protection and future ecological reconstruction of natural corridors (Fig. 3) between important centers will be essential to allow continued species radiation because climatic shifts may displace species' ranges (in isolated parks great extinction will occur); evolution proceeds from centers of radiation outward through

sequences of contiguous habitats latitudinally and altitudinally and there become disrupted from time to time allowing speciation.

Evolutionarily dynamic lineages today create future biodiversity. Such lineages are the cornerstone of natural environmental health. Science has the philosophy and tools to detect these lineages through phylogenetic systematics. Conservation strategy can use the patterns detected in cladistic studies to defend contemporary centers of radiation from destruction on the premise that today's maximum biodiversity, as well as tomorrow's, are in and stem from such centers. Acceptance of a nonhuman yardstick to measure environmental health—that is, evolutionary processes—and implementation of a scientific approach in conservation policies will provide a strategy to achieve a lasting stability for global environmental health because the basis for conservation will not be tied to the whims of human culture. The goal of conservation strategy should be the protection of future maximum biodiversity as well as preservation of contemporary species of human interest.

REFERENCES AND NOTES

1. J. A. McNeely *et al.*, *Conserving the World's Biological Diversity* (International Union for the Conservation of Nature, Gland, Switzerland, 1990).
2. W. V. Reid and K. R. Miller, *Keeping Options Alive: The Scientific Basis for Conserving Biodiversity* (World Resources Institute, Washington, DC, 1989).
3. D. M. Raup, in *Biodiversity*, E. O. Wilson, Ed. (National Academy Press, Washington, DC, 1988), pp. 51–57.
4. T. L. Erwin, in *Taxonomy, Phylogeny and Zoogeography of Beetles and Ants: A Volume Dedicated to the Memory of Philip Jackson Darlington Jr., 1904–1983*, G. E. Ball, Ed. (Junk, The Hague, 1985), pp. 437–472.
5. E. O. Wilson, *Am. Nat.* **95**, 169 (1961).
6. W. Hennig, *Phylogenetic Systematics* (Univ. of Illinois Press, Urbana, 1966).
7. G. Nelson and N. I. Platnick, *Systematics and Biogeography: Cladistics and Vicariance* (Columbia Univ. Press, New York, 1981).
8. M. G. Pogue and M. F. Mickevich, *Cladistics* **6**, 319 (1990).
9. T. L. Erwin and M. G. Pogue, *Proc. Brazilian Acad. Sci.* (1988), pp. 161–188.
10. T. L. Erwin, *Am. Entomol.*, in press.
11. R. A. Mittermeier, in *Biodiversity*, E. O. Wilson, Ed. (National Academy Press, Washington, DC, 1988), pp. 145–154.
12. R. E. May, *Nature* **347**, 129 (1990).
13. R. I. Vane-Wright, C. J. Humphries, P. H. Williams, *Biol. Conserv.* **55**, 235 (1991).
14. I thank B. D. Farrell, W. N. Mathis, R. J. McGinley, M. G. Pogue, and F. C. Thompson for helpful comments, G. L. Venable for the illustrations, and Smithsonian Institution Programs BIOLAT, Neotropical Lowlands Research Project, and Scholarly Studies for funding that led to the concepts developed in this 18th contribution to the BIOLAT Series.

Balancing Species Preservation and Economic Considerations

HAROLD J. MOROWITZ

HOW MUCH IS A SPECIES WORTH? WE GENERALLY TAKE AN anthropocentric view of that question. The species *Homo sapiens*, as judged by the lives and well-being of individuals, is infinitely precious in our public ethic. A tiny arachnid, found only in the sands of Suvarov Islands, isolated in the mid-Pacific, is likely to get a much lower rating. The question becomes, "What is the value of a given species to human society?" Once the term "value" is introduced, the question moves to economics and ethics, both of which use that construct, but in very different senses. From a narrow economics point of view, we need a monetary metric of a species value to balance benefits against costs of preservations (1). Viewed from environmental ethics no such direct measure is possi-

ble (2). These considerations apply to ecosystems as well as to individual taxa. We are often left trying to balance the "good" of ethics with the "goods" of economics.

Some conservationists have argued for the virtue of the preservation of almost all species (3). There are techno-optimists who downplay the species problems (4). Extremist advocates of artificial intelligence envision a silicon chip-based "life" to succeed carbon-based humans (5). Some traditional economists might argue that the amount we are collectively willing to expend to preserve a species is an appropriate utility measure. But traditional theory does not deal effectively with goods not exchanged in organized markets. Free air and water pollution are examples of this approach. One senses that there has been far too little dialogue between environmental biology and economics.

The National Academy Forum on Biodiversity (3) devotes 30 of its 500 pages to economic issues, and the newly formed Society for Ecological Economics has begun to approach value problems. But one senses that there is not a full engagement of either of the contributing disciplines. Economics students are not required to study biology, and the curriculum of ecologists does not usually include economics. As noted in a recent business publication, "Environmental economics has been relegated unfairly to the mar-

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