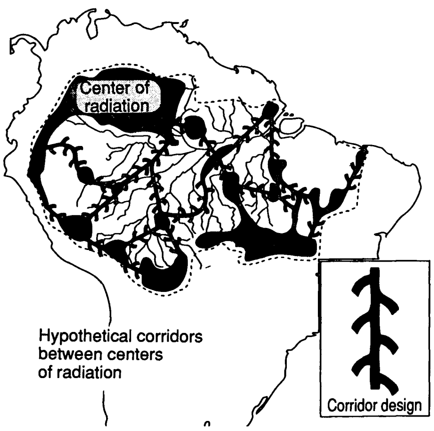

Fig. 3. Future corridors of ecological reconstruction between hypothetical centers of radiation—for example, in the Amazon Basin, to allow species movements and radiation. Inset is a design for a corridor that maximizes soil and habitat types in small areas.

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.

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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 possible (*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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gins of the economic community" (*6*). Difficult concepts such as the irreversibility accompanying species extinctions, the preferences of future generations, the problem of present benefits and future costs, and the distinction between commodity value and moral value render the economic mensurability of species preservation extremely difficult. Some conservationists argue that such an approach is wrong from a philosophical perspective (*2*). We are often left contrasting what is economically beneficial to individuals versus what is beneficial to society as a whole.

A few ideas are basic to our considerations. Species have almost certainly existed for over 3.7 billion years. It is in the nature of these taxa to arise, flourish for a time, and perish. For many biological groupings, the majority of species are no longer extant. Even the notion of what constitutes a species is not universally agreed on.

At some time in the last several million years, along the evolutionary line of hominids, reflective thought arose, coming to fruition in *Homo sapiens*. The appearance of a species with this novel noetic property is a discontinuity, a biological event of catastrophic impact and, of necessity, it profoundly changed the development of local and global ecosystems. In our reductionist fervor we sometimes have been remiss in underestimating the effect of reflective thought on global ecology. Environmentalists have not focused on how strange and different organisms human beings really are.

The agrarian revolution during the past 10,000 or more years converted vast land areas from forests, savannahs, and plains to fields and pastures. The large accompanying species loss was an inevitable sequela of the emergence of human civilization as we know it. This epoch, which was devastating in terms of biological diversity, is nevertheless referred to as "the humanization of the earth" by Dubos (7). Human society in the present context is inextricably intertwined with agricultural monoculture, the worst of all worlds from a diversity perspective. As the Irish potato famine and the desertification of the Sahal show, agricultural practices may also have devastating social and economic consequences. Humans, because of their engineering abilities, create another geosphere, the technosphere, to add to the traditional lithosphere, hydrosphere, atmosphere, and biosphere.

The continuing growth of human population requires ever more land for housing and agriculture, resulting in progressively increased habitat destruction. The conclusion is clear: the amount of unexploited lands and waters will decrease with increasing human population. Although the exact function is uncertain, the sign of the first derivative is ensured. Similarly, the total number of planetary species will be some monotonic function of unused habitats. Ergo, biodiversity decreases with increasing human population.

No discussion of managing global habitats and preserving species can avoid the population imperative. Ignoring this problem, whether for political, ideological, or theological reasons, which is the present stance of many world political leaders, is a policy that inevitably leads to habitat loss and species depletion. There has been an unwillingness to face the conclusion that environmental planning and concern for conservation in the absence of population control are tasks worthy of the metaphor of Sisyphus.

Following agriculture, a second great change has occurred: the industrial revolution and burning of fossil fuels. In chemical terms, for several hundred million years there has been a dehydration and reduction of buried biogenic CH_2O converting it to CH_4, CH_2, and C. The sudden reversal of this process to yield CO_2 is a major global consequence of industrialization. The acquisition and use of fossil fuels has resulted in habitat changes and loss of species.

From a direct economic perspective, the most severe changes in biota would be those that alter the global climate or geochemical distribution of essential materials or impact severely on cosmopolitan taxa. For example, loss of the genus *Rhizobium* (a most unlikely happening) would change the entire global nitrogen balance to a degree that would require industrial nitrogen fixation or the farming of reduced nitrogen, which are clearly energetically expensive operations. If the loss of the Amazon rain forest were to lead to widespread deleterious climatological effects or major global mineral nutrient imbalance, then this would similarly be of direct economic importance.

Let us examine some of the more difficult to evaluate public goods. Species preservation has been argued from the viewpoint of potential future sources of natural products. Here the costs might be compared with those of the chemical research and biotechnology required to synthesize and test new compounds and produce them industrially. This is a case where conservationists are making direct economic assertions whose strength is subject to analysis by economic methods. Even this is complicated by the unknown future value of such commodities as tropical plant–based medicinals, which are now a rapidly expanding growth industry (*8*).

Much more difficult to deal with as a public good is the value of knowledge. A lost species may potentially possess some novel biological features that will forever be inaccessible to study. For example, the sperm and blue whales and the elephants, as the largest marine and terrestrial mammals, certainly merit extreme efforts of preservation on grounds of physiological uniqueness. It is difficult to put knowledge arguments in economic terms, but such knowledge is certainly part of my utility function and ultimately may influence agriculture, medicine, and industrial processes.

On the grounds just discussed, I would also argue for the careful conservation of primates, prosimians, and their immediate predecessors. The transition along the primate line to hominids is an ill-understood, vastly profound, and clearly globally overwhelming phenomenon. The anatomy, physiology, and behavioral biology of the primates are clearly major avenues to understanding aspects of ourselves and our culture.

The search for physiological uniqueness centers on larger organisms, whereas the search for novel biochemical features extends over all sizes. In the center of the size range is a vast array of insect species dominated by the Coleoptera and Diptera. In any case, if an argument is to be made to undertake the study of economic costs of preserving an individual species, the uniqueness or lack of uniqueness of that taxon should certainly be a component of the reasoning. Biodiversity per se may be of great intellectual importance to biologists, but to a broader society the argument hinges on something of more public value than our desire as biologists to understand all life, as laudable as that desire might be. The politics of species preservation should perhaps be shifted to the politics of habitat preservation.

Another group of taxa have a special but difficult to assign value because of cultural reasons or because they inspire a sense of awe and wonder. This has been referred to as amenity value. The mammals of Africa, the redwood trees of the western United States, and the Antarctic penguins are in this category. It is hard to develop a metric of awe and wonderment, yet it clearly is a factor in human response. If a habitat draws paying tourists to observe the flora and fauna, then we have some measure of human response. An example of a culturally significant species is the American bald eagle, which has acquired a symbolic importance far beyond the purely biological.

In dealing with issues of knowledge or cultural association, we clearly deal with public goods or collective goods as distinguished from the private goods of market economics. Here the market analogy becomes less useful and the invisible hand has to be replaced by aspects of the social compact. Regulation may be introduced for other than economic reasons, but this requires some kind of consensus. Bossons (*9*) argues,

> Difficulties created by the public nature of ecological resources and their externalities suggest that the approach needed to rationalize protection of these resources must be reversed with respect to the approach used by competitive markets to satisfy consumers' demands.

Many environmental battles are being fought on these grounds.

There is a school of economic analysis (*10, 11*) that maintains that environmentally unsound practices are often economically unsound and involve governments fostering habitat destruction to protect politically influential industries. This leads to (*11*) "the use of limited natural resources at practically no cost." A number of examples are given (*10*) from the logging industry in the United States. The author maintains that in many cases the government is in fact subsidizing the clear-cutting of forests to produce a product that would be noncompetitive in the market without the subsidy. This is the reverse of the role a government should play in dealing with public goods.

What becomes clear is that it is not true that a species is a species is a species. The debate about preservation and management versus letting nature take its course must be argued for each taxon and habitat in some detail based on an understood and agreed upon way of assigning values. If preserving a species is to be used as a cover statement for preserving a habitat, it would be better to get the actual reasons up front so they can be debated on merits. Except in those very few cases where cost and benefit have calculable monetary values, conversion factors will have to be developed in terms of more abstract benefits. As has been pointed out by Baden (*12*), "not all values can be denominated on a spreadsheet."

It is necessary to stress that none of the trade-offs necessary to establish the relations between different value systems can be accomplished until biologists, economists, and technologists are willing and able to carry out discussions. A rational approach to problems demands this kind of communication. One would envision that the recently proposed National Institute for the Environment would be a locus for this activity, which at present lacks a home.

At the beginning of this century, humankind inherited a great diversity of biota. The industrial revolution inevitably compromised habitats and led to large-scale extinctions. We have reached a stage where there is general agreement that ecosystems, including the global ecosystem, must be managed (*13*). This requires, at the very least, more effort devoted toward an improved understanding of ecological theory. It also urgently requires some national and international consensus as to the goals of that management. Public goods are clearly the province of governments.

We would be remiss not to repeat the assertion that as human population goes up, biological species diversity goes down. We might be able to moderate the rate of decline, but we cannot fend off the inevitable. As species number goes down, we might, of course, change our valuation system and subsequent responses; they are, after all, cultural, not metaphysical. The answer to "How much is a species worth?" is "What kind of world do you want to live in?"

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Extinctions: A Paleontological Perspective

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THE FOSSIL RECORD IS RICH IN EXTINCTION: THE STAGGERing diversity of the present-day biota (*1*) represents a minute fraction of the taxonomic and morphologic variety that has populated the earth since the explosive diversification of multicellular organisms at the beginning of the Phanerozoic. Compilation and statistical analysis of temporal ranges of fossil taxa have verified that extinction intensities per unit time have varied widely, with a continuum from low to high intensities. Background extinction is recognized operationally as the troughs between extinction maxima in time series, and may involve the loss of only a few species. At higher intensities, extinctions may affect only a narrow subset of species (as in the late Pleistocene megafaunal extinction), or may be taxonomically and geographically pervasive (as in the mass extinctions as currently defined) (*2–7*). Paleontologists have learned much about the timing, magnitude, selectivity, and recovery patterns of the major extinction events (*8*), but the implications of these data for present biodiversity are still not fully understood. The fossil record is, however, our only direct source of information on how biological systems respond to large-scale perturbations and thus can provide important insights into potential outcomes if habitat destruction or climate change proceeds unchecked (*9, 10*).

The most basic observation is simply that mass extinctions have happened: irreversible biotic upheavals have occurred repeatedly in the geological past. Marine and terrestrial biotas are not infinitely resilient, and certain environmental stresses can push them beyond their limits (*11*). This basic message derives not only from the fossil record of the five major mass extinctions of the Phanerozoic, but from smaller events like the end-Cenomanian and end-Eocene events (Table 1), and regional extinctions like the Pliocene loss of more than 50% of northeastern Atlantic and 75% of northwestern Atlantic bivalve species (*12*). The major mass extinctions have apparently mediated faunal replacements that were once attributed to a more classically Darwinian competitive process (*13, 14*): dominant groups decline or disappear and previously unimportant taxa rise to prominence in the aftermath, as seen in the successive reef biotas of the Phanerozoic (*15, 16*) and the successive terrestrial vertebrate dynasties from mammal-like reptiles to dinosaurs to mammals (*13*). Terrestrial plants have sometimes been described as exempt from ancient mass extinctions (*17*), but this is true only at the highest taxonomic levels. Detailed work on species and genera, for example, suggests that the end-Cretaceous extinction removed more than 50% of plant species and may have played a pivotal role in structuring the Cenozoic flora, at least in the Northern Hemisphere (*18*).

Survival of species or lineages during mass extinctions is not strictly random, but it is not necessarily closely tied to success during times of normal background extinction. Analyses of selectivity during mass extinctions are still scarce, and patterns emerge more

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