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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Table 1. Extinction intensities at the genus and species level for the five major mass extinctions of the Phanerozoic and selected smaller post-Paleozoic extinction events. Generic values are calculated empirically from the marine fossil record (*3*); species loss inferred by rarefaction from generic data (*3, 65*). Age values from Harland *et al.* (*42*).

Extinction	Age ($\times 10^6$ years)	Genera (%)	Species (%)
Late Eocene (Priabonian)	35.4	15	35 ± 8
End-Cretaceous (Maastrichtian)	65.0	47	76 ± 5
Late Cenomanian	90.4	26	53 ± 7
End-Jurassic (Tithonian)	145.6	21	45 ± 7.5
Pliensbachian	187.0	26	53 ± 7
Late Triassic (Norian)	208.0	47	76 ± 5
Late Permian	245.0	84	96 ± 2
Late Devonian (Frasnian)	367.0	55	82 ± 3.5
Late Ordovician (Ashgillian)	439.0	61	85 ± 3

clearly at lower taxonomic levels than at high ones, but some generalizations can be drawn. Among terrestrial vertebrates, for example, large-bodied lineages appear to suffer more severely than small-bodied forms {witness the end-Cretaceous dinosaurs [though juvenile and small adult forms also vanished (*19*)] and the end-Pleistocene megafauna (vertebrates over 44 kg)}; this makes biological sense, in terms of such factors as expected population sizes and densities (low), home range requirements (large), generation times (long), and trophic requirements (large) (*20*). The ecological consequences of the removal of these large vertebrates are only beginning to be explored, and the exploration requires reciprocal neontological-paleontological study, but may be far-reaching. In part on the basis of ecological research in Africa, the one continent that retains much of its Pleistocene megafauna, Owen-Smith (*21*) suggests that the end-Pleistocene extermination in North America of the species most attractive as human prey, such as mastodon and mammoth, would have brought extensive vegetational changes that in turn would explain the concomitant disappearance of so many other vertebrates. Such cascading ecological effects have long been suspected for the major mass extinctions [for example, the probable collapse of marine food chains with the end-Cretaceous phytoplankton crisis (*22*)], and may provide a useful model for the potential consequences for local or total extermination of present-day elephants and some of the other African megaherbivores (*23*). Controlled ecological experiments are still the most powerful way to predict responses of particular communities to species removals (*24*), but this approach would be particularly valuable if designed around removal of species likely on demographic or paleobiological grounds to be most extinction-prone.

Among marine invertebrates, where the fossil record is more completely known and more readily quantified (*25*), at least one strong generalization has emerged: widespread genera preferentially survive mass extinctions, whereas geographically restricted genera are particularly vulnerable (*14, 26–29*); during background extinction geographical range more demonstrably plays a role at the species level (*30*). Some factors that contributed to genus survival during background times, such as species richness, were ineffective during the end-Cretaceous mass extinction, so that molluscan and echinoderm taxa were lost that ordinarily were extinction-resistant (*14, 26, 31*); the same holds for early Paleozoic trilobites (*28*), late Devonian corals (*32*), and Paleozoic ammonoids (*33*) but not, apparently, for end-Permian gastropods (*29*). Major extinction events also preferentially or indifferently removed taxa normally at low risk among Paleozoic bryozoans (*34*), Late Cenozoic Foraminifera (*35*), and Late Cenozoic bivalves (*35*). Evidence is thus accumulating that taxa and morphologies may have been lost not because they were poorly adapted by the standards of background processes, but because they occurred in lineages lacking the environmental tolerances or geographic distributions necessary for surviving the mass extinction.

The paleontological data, then, corroborate suggestions (*9, 10*) that present-day perturbations are likely to impinge most heavily on rare, geographically restricted species, and can be indifferent to adaptations honed by prolonged intervals of natural selection under background extinction. In the face of ongoing habitat alteration and fragmentation, this implies a biota increasingly enriched in widespread, weedy species—rats, ragweed, and cockroaches—relative to the larger numbers of species that are more vulnerable and potentially more useful to humans as food, medicines, and genetic resources. However, we have little means of translating paleontological data into predicted rates or patterns of species loss for any given present-day locality or region. Data are needed on living species that allow direct comparison with the fossil record. For example, frequency distributions of geographic ranges for local faunas and floras would provide a framework for inferring the most vulnerable taxa, and for assessing possible impacts of losses at the more extinction-prone end of the geographic range spectrum. Such an approach will, of course, provide only a first approximation of extinction probability; some species, for example, are widespread but have narrow requirements (*36*), such as a herbivore dependent on a complex of geographically restricted (and thus extinction-prone) plant species. Nevertheless, the high rate of habitat disturbance or fragmentation, particularly in the tropics, lends urgency to the development of efficient approaches to estimating potential biotic consequences.

The fossil record also suggests that tropical biotas are the most vulnerable to extinction (*37*). The general impression, however, needs to be more fully explored: few data are available for terrestrial organisms, and the underlying marine data derive mainly from the striking demise of reef communities at each of the major mass extinctions (*15, 16*), combined with some evidence for relatively low extinction intensities at high latitudes (*38*). Whether this boom-and-bust history reflects the vulnerability of the tropical marine biota in general, the vulnerability of the reef community in particular, or a chain of events put in motion by the extinction of geographically restricted species, as elsewhere on the globe, is not known (*14*). Reef biotas survived Pleistocene climate and sea-level fluctuations with few losses (*39*), but this may be an unreliable model for the present-day situation. Pleistocene reef species depended not upon withstanding in situ stresses but on shifting to or persisting in benign refugia (*39, 40*) now becoming increasingly scarce as human activities impinge on these environments.

Biotic recoveries after mass extinctions are geologically rapid but immensely prolonged on human time scales. New reef communities are not recognizable until 5 million to 10 million years after extinction events (*15*), and Talent (*16*) argues that the re-invasion—and re-invention—of these habitats postdates by millions of years the slackening of the environmental perturbations associated with the demise of the preceding community. Further testing is needed, but the delay evidently reflects constraints on the evolution of species or assembly of communities capable of occupying these habitats rather than on continuing environmental stresses. Similarly, marine bivalves show episodes of accelerated diversification in the wake of mass extinctions, with recovery to pre-extinction levels of generic diversity requiring at least 10 million years (*41*). Whatever the exact magnitude of present-day diversity losses, rebounds in the fossil record suggest that they will not be recouped in the next thousand years, even in the absence of further disturbance. Comparative analysis of geologic intervals with intense turnover but modest drops in standing diversity might reveal taxon-specific or habitat-specific thresholds below which "instantaneous recoveries" are not possible. Such estimates could be used to weigh the risk of incurring truly long-term consequences under alternative management schemes.

Comparisons between present conditions and the fossil record are severely hindered by problems of temporal and taxonomic scale, and by a basic nonequivalence between the kinds of data available for the two systems. Reliable predictions on the decade or century scale are urgently needed today, but temporal resolution in the pre-Pleistocene fossil record is at least two to three orders of magnitude coarser, due to problems such as gaps in the record and vertical mixing of successive populations (*42*). Thus, even truly instantaneous events cannot be distinguished from processes encompassing 10^5 to 10^6 years, particularly on a global scale. Moreover, high-resolution data suggest some measurable duration for most, if not all, major extinctions. Even the end-Cretaceous event, the one most likely to have been triggered suddenly by bolide impact or other environmental shock, apparently involved at least 10^4 to 10^5 years of oceanographic and atmospheric turmoil when analyzed at single sites (an approach that sacrifices global generality for refined local resolution) (*43*). The best-dated extinction of the geologic record, the terminal Pleistocene extinction of large mammals, is currently estimated as spanning about 9,000 years (with onset about 18,000 years ago) (*44, 45*).

The best paleontological extinction data, in terms of geographic coverage and temporal resolution, are for marine invertebrates and microplankton. Most workers consider large databases to be more robust to sampling biases when compiled at the genus level or above, and many argue that the behavior of genera is useful as a damped proxy for species-level processes (*3, 46*). These factors alone would hamper quantitative comparisons to present-day extinctions, but a subtler bias is also at work: the extinctions detected by paleontologists primarily involve taxa that are more widespread and abundant (and thus more likely to be fossilized) than the extreme endemics that constitute some fraction of present-day estimates for endangered tropical species. Many uncommon, localized taxa do enter the fossil record, but species such as those restricted to the now deforested Centinela Ridge, Ecuador [≤ 20 km^2 (*47*)], would almost certainly fail to be fossilized or collected, and this renders overall comparisons to fossil data problematic. Estimated paleontological background rates are so low [averaging only about 1 to 10% per million years for marine invertebrate species (*48*) but less fully analyzed for terrestrial animals or plants] that tropical extinctions corrected to their potential fossil record would still probably exceed paleontological background rates, but this question requires careful analysis.

One approach to scaling present-day extinction estimates to the fossil record would be to assess how many living species and genera described thus far (which in turn are just a fraction of the 5 million to 30 million living species estimated) actually, or even potentially, have a fossil record. More than 77% of 700 species of shelly marine mollusks of the Californian province occur as Pleistocene fossils (*49*), and comparable proportions probably obtain for vertebrates and plants, particularly for pollen taxa. Given a particular scale of perturbation, then, what is the expected fate of those groups for which the fossil record provides the most robust predictions?

Finally, the disparity of the unknowns in the two systems also hinders detailed use of the fossil record to predict present-day biodiversity losses and their consequences. Paleontologists have a partial record of taxon loss in time and space, and attempt to infer the nature of the disturbances that caused the observed magnitudes and patterns of differential extinction. Linkages between a particular extinction episode and climatic or other potential forcing factors are hypotheses to be tested. In contrast, biologists have partial data on environmental disturbances such as rain forest conversion and attempt to infer or predict magnitudes and patterns of extinction. Again, compiling data on living species that are analogous to paleontological data might be the most efficient means of generating rigorous interdisciplinary extrapolations.

All of these problems are minimized in the youngest part of the fossil record: the last 5.2 million years since the start of the Pliocene, with their oscillations between glaciations and global warming trends, are being explored in increasing stratigraphic, geochemical, and paleobiological detail (*12, 50*). Data on differential survivorship and geographic shifts of late Tertiary vertebrate and plant species in response to increasing aridity and habitat patchiness (*50, 51*) should be useful in inferring potential effects of present-day perturbations. The analogy is imprecise because the late Tertiary changes seem tied ultimately to the onset of global cooling, an unlikely scenario for the immediate future, but faunal and floral dynamics can still be used to good predictive effect given the diversity of present and impending environmental alterations independent of the overall vector of global climate change. Further, the repeated oscillations between glacial and interglacial states that characterize global climates over the past 2 million years provide replicated natural experiments on biotic consequences of rapid shifts in global temperature and rainfall patterns.

The past 50,000 years in particular offer extraordinary opportunities for predicting upcoming biotic changes. Time resolution is on the order of centuries, geochemical tracers permit fine-scale calibration of paleotemperature and other factors, and many of the plant and animal species are still extant, so that past performances can be projected into the future with some confidence. In addition to encompassing the end-Pleistocene extinction of large terrestrial vertebrates (*45*), this interval provides invaluable data on the behavior of species and communities in response to climatic changes, most notably the most recent post-glacial global warming trend. The most important message of this still underexploited record is that ecological communities do not respond as units to environmental change. Pollen and skeletal data show that species are highly individualistic in their behavior, so that few, if any, modern terrestrial communities existed in their present form 10,000 years ago. Instead, they originated in piecemeal fashion by means of shifts in abundance or geographic range of their constituent species and will presumably continue to change composition in response to anthropogenic or natural climatic changes.

The individualistic behavior of terrestrial species in response to Pleistocene and Holocene climate changes is evidently a general phenomenon, known for plants in eastern and western North America (*52, 53*), Europe (*54*), South America (*55*), Australia (*56*), and Africa (*57*), North American vertebrates (*58*), and invertebrates (*59*). This fundamental paleontological insight cannot be ignored in designing nature reserves (*60*): reserves must be sufficiently large and environmentally complex to accommodate the array of disparate geographic range shifts that any climatic change will evoke from the resident species assemblage. Any other attempts to anticipate species behavior—cultivars or pest species, for example—must take these discoveries into account as well.

Late Pleistocene–Holocene extinctions are still controversial, but most authors now assign humans at least an accessory role for the end-Pleistocene megafaunal extinctions (*61*). The Holocene fossil or archeological record has also revealed significant extinction due primarily or exclusively to pre-European human disturbance, particularly in island biotas [for example, more than 50% of the avifauna in Hawaii and other Polynesian islands (*62*), and 49% of West Indies land mammals (*63*)]. These data force a substantial upward revision of estimated post-Pleistocene human impacts and offer rich possibilities for testing hypotheses on causes and consequences of special loss. They also undermine attempts to predict biotic responses to habitat reduction or fragmentation, which are commonly based on species-area relations in modern island biotas that are assumed to be at evolutionary equilibrium. In any case, the fossil data on individualistic species behaviors support arguments that habitat diversity is more important than area per se in refuge design (*60, 64*).

The lessons of the past are inevitably blurry and at a coarse scale. At the present state of knowledge, the fossil record is more revealing of potential long-term consequences than of immediate solutions. However, the history of life on Earth provides an array of worst-case scenarios—including even the mildest of the extinction events in Table 1—that are sufficiently spectacular to militate against inaction. Coordinated research on fossil and extant biotas should yield very real benefits for understanding, anticipating, and perhaps managing the biological changes driven by human activities.

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