The Future of Biodiversity

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Recent extinction rates are 100 to 1000 times their pre-human levels in well-known, but taxonomically diverse groups from widely different environments. If all species currently deemed "threatened" become extinct in the next century, then future extinction rates will be 10 times recent rates. Some threatened species will survive the century, but many species not now threatened will succumb. Regions rich in species found only within them (endemics) dominate the global patterns of extinction. Although new technology provides details of habitat losses, estimates of future extinctions are hampered by our limited knowledge of which areas are rich in endemics.

Debates about the consequences of human population growth are not new. Our numbers have increased dramatically since Malthus but so has our technology (*1*). Will technical ingenuity keep pace with increasing population problems? Ingenuity can replace a whale-oil lamp with an electric light bulb, but not the whales we may hunt to extinction. Species matter to us (*2*). How fast we drive them to extinction is a matter of our future. Critics consider high estimates of current and future extinction rates to be "doomsday myths," contending that it is the "facts, not the species" that are endangered (*3*). Here, we review these estimates.

Extinctions have always been a part of Earth's history. So what is the background rate of extinction: how fast did species disappear in the absence of humanity (*4*)? A summary of 11 studies of marine invertebrates suggests that fossil species last from 10^6 to 10^7 years (*5*). For ease of comparison, we use the number of extinctions (E) per 10^6 species-years (MSY) or E/MSY. If species last from 10^6 to 10^7 years, then their rate of extinction is 1 to 0.1 E/MSY.

These estimates derive from the abundant and widespread species that dominate the fossil record. The species most prone to current extinction are rare and local. Moreover, we emphasize terrestrial vertebrates in our discussions of current extinctions. There are only two studies of their fossils (*5*), and these suggest high background rates (~1 E/MSY). Interestingly, we can supplement these estimates from our knowledge of speciation rates. These could not be much less than the extinction rates, or the groups would not be here for us to study.

Molecular phylogenies are now produced rapidly and extensively. There is one for 1700 bird species (*6*). Using the relative time axis of molecular distances, we can elucidate the patterns of species formation. Models in which every lineage has the same, constant probability of giving birth to a new lineage (speciation) or going extinct (death) permit estimation of the rate parameters (*7*). The rich details of this approach offer hope in testing for important factors controlling the relative rates of background speciation and extinction. Obviously, absolute rates require accurately dated events, such as the first appearance of a species or genus in the fossil record. There are genetic distance and paleontological estimates of divergence times for 72 carnivore and 14 primate species or subspecies (*8*). Given their importance as a benchmark against which to compare modern extinction rates, we plead for more absolutely timed accounts.

How Many Species Are There?

Any absolute estimate of extinction rate requires that we know how many species there are. In fact, we do not. May (*9*) shows that the problems of estimating their numbers are formidable. Only ~10^6 species are described and <10^5—terrestrial vertebrates, some flowering plants, and invertebrates with pretty shells or wings—are popular enough to be known well. Birds are exceptional in that differences in taxonomic opinion [~8500 to 9500 species (*6*)] far exceed the annual descriptions of new species (~1). Most species are as yet undescribed in every species-rich group (Fig. 1). Major uncertainties lie in those groups in which we have scant or conflicting evidence of very high diversity. There are ~10^6 described insects, yet estimates range from ~10^7 to nearly 10^8 species. Some potentially rich communities, such as the deep-sea benthos, have been sparsely sampled.

How can we be confident in our extrapolations of extinction rates from the <10^5 well-known species to the ~10^6 described, or to the conservative grand total of ~10^7 (*5*)? If extinction rates in diverse taxa and regions are broadly similar, then they are

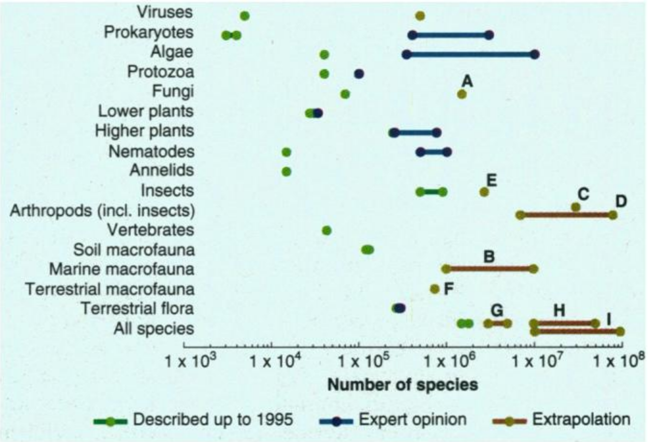

Fig. 1. Numbers of described species and estimates of species numbers, including expert opinions of taxonomic specialists (*12*) and various extrapolations (*26*). (**A**) The British ratio of 6 fungi species:1 plant species and a world total of 2.5 × 10^5 plant species suggests ~1.5 million species of fungi worldwide. (**B**) A world total of 10^6 to 10^7 species of marine macrofauna comes from the accumulation of new species along sample transects. (**C**) A large sample of canopy-dwelling beetles from one species of tropical trees had 163 species specific to it. There are 5 × 10^4 tree species, and so 163 × 5 × 10^4 ≈ 8 × 10^6 species of canopy beetles. Because 40% of described insects are beetles, the total number of canopy insects is 2 × 10^7. Adding half that number for arthropod species on the ground gives a grand total of 3 × 10^7. (**D**) If only 20% of canopy insects are beetles, but there are at least as many ground as canopy species, then the grand total is 8 × 10^7. (**E**) Some 63% of the 1690 species on ~500 Indonesian tree species were previously unrecorded. The ~10^6 described insect species thus suggest a total of 2.7 × 10^6 species. (**F**) Across many food webs, there are roughly three times as many herbivores and carnivores combined as there are plants. This resulting estimate of terrestrial animal species, ~7.5 × 10^5, is certainly too low, because published food webs omit many species. (**G**) There are about two tropical bird and mammal species for each temperate or boreal species. Yet, of the ~1.5 × 10^6 described species, about one-third is tropical. The prediction of 3 × 10^6 species is an underestimate, because not all temperate species are described. (**H**) There is a linear increase in species numbers with decreasing body size. Below a threshold level, however, the numbers drops, perhaps because of sampling bias. If the true pattern remained linear, there would be 1 × 10^7 to 5 × 10^7 species. (**I**) We added the more detailed estimates for the numbers of species in the largest groups.

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likely to be representative. If we understand the underlying mechanisms, we may find they operate universally.

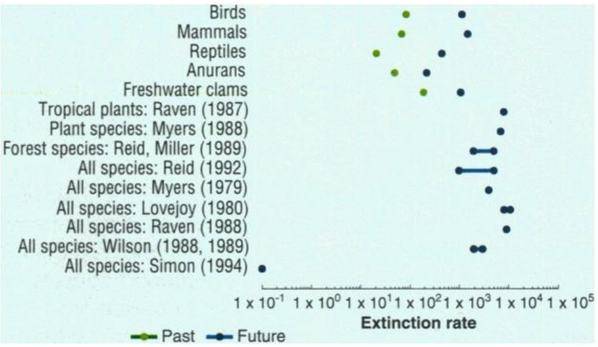

Fig. 2. Estimates of extinction rates expressed as extinctions per million species-years. For birds through clams, we derive past rates from known extinctions in the last 100 years; we derive future rates by assuming that all currently threatened species will be extinct in 100 years. The latter rates are much higher than the former but are still far too low. The remaining estimates are previously published (*1, 16, 27*). Myers (1979) (*27*) assumes an exponential increase in the number of extinctions. Myers (1988) (*16*) assumes the loss of a small number of areas rich in endemics. With the exception of Simon, the rest are estimates based on the relation between habitat loss and species loss. Simon's claims (*1*) of one (or a few) species per year (out of a conservative total of 10^7 species) are not scientifically credible.

The Past as a Guide to the Future

Unambiguous evidence of human impact on extinction comes from before-and-after comparisons of floras and faunas (*10*). Polynesians reached the planet's last habitable areas—Pacific islands—within the last 1000 to 4000 years. The bones of many bird species persist into, but not through, archaeological zones that show the presence of humans. No species disappeared in the longer intervals before the first human contact. Adding known and inferred extinctions, it seems that with only Stone Age technology, the Polynesians exterminated >2000 bird species, some ~15% of the world total.

We must infer extinctions, because we will not find the bones of every now-extinct species. From the overlap in species known from bones and those survivors seen by naturalists, sampling theory infers that ~50% of the species are still missing (*10*). Faunal reconstruction affords a second inference. For example, Steadman (*10*) contends that every one of ~800 Pacific islands should have had at least one unique species of rail. A few remote islands still have rails. Others lost theirs to introduced rats in the last century. Large volcanic islands typically lost several species of rails. Accessible islands lost their rails earlier, for every survey of bones from islands now rail-free has found species that did not survive human contact.

High extinction rates also followed the Pacific's colonization by Europeans. Since 1778, the Hawaiian islands have lost 18 species of birds; the fate of 12 more is unknown (*10*). Nor are birds unusual. Of 980 native Hawaiian plants, 84 are extinct and 133 have wild populations of <100 individuals (*11*). Across the Pacific, a predatory snail introduced to control another introduced snail ate to extinction hundreds of local varieties of land snails (*12*).

Nor are Pacific islands unusual: of 60 mammalian extinctions worldwide, 19 are from Caribbean islands (*12*). In the last 300 years, Mauritius, Rodrigues, and Réunion in the Indian Ocean lost 33 species of birds, including the dodo, 30 species of land snails, and 11 reptiles. St. Helena and Madeira in the Atlantic Ocean have lost 36 species of land snails (*12*).

Importantly, extinction centers are not necessarily on islands nor only in terrestrial environments. The fynbos, a floral region in southern Africa, has lost 36 plant species (of ~8500); 618 more are threatened with extinction (*12*). Extinctions of 18 (of 282) species of Australian mammals rival those from the Caribbean; 43 more are threatened (*12*). In the last century, North American freshwater environments lost 21 of 297 mussel and clam species (120 are threatened) and 40 of ~950 fish species (*12*).

This world tour of extinction centers has remarkable features (*12*). Recent extinction rates are 20 to 200 *E*/MSY (Fig. 2)—a small range given, among other things, the uncertainties of whether to average rates over a century or a shorter interval that reflects more recent human impacts. We find high rates in mainlands and islands, in arid lands and rivers, and for both plants and animals. Although we know less about invertebrates, high rates characterize bivalves of continental rivers and island land snails. There is nothing intrinsic to the diverse life histories of these species to predict their being unusually prone to extinction.

What obvious features unite extinction centers? We know the species and places well—as did naturalists a century ago. Importantly, each area holds a high proportion of species restricted to it. Such endemics constituted 90% of Hawaiian plants, 100% of Hawaiian land birds, ~70% of fynbos plants, and 74% of Australian mammals (*12*). In contrast, only ~1% of Britain's birds and plants are endemics (*12*). Remote islands are typically rich in endemics, but so are many areas within continents (*13*). Past extinctions are so concentrated in small, endemic-rich areas that the analysis of global extinction is effectively the study of extinctions in one or a few extinction centers (*12*). Why should this be?

Random extinction is the simplest model. Some species groups and some places will suffer more extinctions than others, but generally the more species present, the more there will be to lose. This model does a poor job of predicting global patterns. If island birds were intrinsically vulnerable to extinction, then Hawai'i and Britain with roughly the same number of species of breeding land birds (~135) would have suffered equally. Hawai'i had >100 extinctions, Britain only 3 (*12*). Nor is the number of species an area houses a good predictor of the total extinctions. Islands house few species and suffer many extinctions.

Imagine a cookie-cutter model where some cause destroys (cuts out) a randomly selected area. Species also found elsewhere survive, for they can recolonize. But some of the endemics go extinct, the proportion depending on the extent of the destruction. We do not assume that island biotas are intrinsically more vulnerable than mainlands. For random species ranges, the number of extinctions correlates weakly with the area's total number of species, but strongly with the number of its endemics. By chance alone, small endemic-rich areas will contribute disproportionately to the total number of extinctions.

This model is consistent with known mechanisms of extinction. Habitat destruction cuts out areas, as the model implies. Introduced species also destroy species regionally. Species need not be entirely within the area destroyed to succumb to extinction: The populations outside may be too small to persist (*14*). Moreover, across many taxa, range-restricted species have lower local densities than widespread species (*15*). The former are not only more likely to be cut in the first place, but their surviving populations will have lower densities and thus higher risks of extinction than widespread species. This entirely self-evident model emphasizes the localization of endemics—Myers' "hot spots" (*16*)—as the key variable in understanding global patterns of recent and future extinctions.

Predicting Future Rates of Extinction

Projecting past extinction rates into the future is absurd for no other reason than that the ultimate cause of these extinctions—the human population—is increasing exponentially. For vertebrates, we have worldwide surveys of threatened species

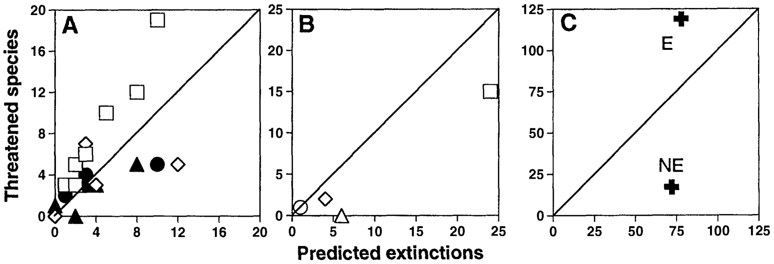

Fig. 3. The numbers of species currently threatened with extinction plotted against the numbers of species predicted to become extinct. Squares, Philippines; circles, North Wallacea; diamonds, Greater Sundas; triangles, Lesser Sundas. The predictions use satellite estimates of remaining forest cover and the relation between species numbers and area. (**A**) For the subset of species endemic to single islands, these numbers match; they straddle the graph's diagonal. (**B**) For the subset of species that are endemic to several islands within each region, the predicted extinctions consistently exceed the numbers of threatened species. (**C**) When we combine the species found on one or several islands (E) across the entire region, the predictions based on forest losses (78) are slightly smaller than the number of threatened species (119). The remaining subset comprises widely occurring species (NE). Their predicted extinctions (72) far exceed the few (17) actually threatened with extinction. Predictions of extinctions from habitat loss must be scaled to the number of endemics the area contains (*23*).

(*12*). Is it reasonable to assume that all these species will be extinct in <100 years, thus making future rates 200 to 1500 *E*/MSY (Fig. 2)?

Some threatened species are declining rapidly and will soon be extinct. Others, not so obviously doomed, have small numbers (<10^2). They risk the demographic vagaries of sex (all the young of a generation being of the same sex) and death (all the individuals dying in the same year from independent causes). For these, both models and empirical, long-term studies of island populations suggest times to extinction on the order of decades (*17*). Population fluctuations, and the environmental vagaries that cause them, drive the extinction of larger populations (>10^2) (*14*). Over 20 years, bird densities can vary 10-fold, and insect densities 10,000-fold (*14*). Ecologists have been slow to combine models and data. Yet even in the absence of a formal analysis, such fluctuations can obviously doom even quite large populations.

Our predictions may err because some threatened species will survive the century (*18*). The more serious problem with our predictions is that species not now threatened will become extinct. For birds—the one group for which we have detailed lists of the causes of threats—limited habitat is the most frequently cited factor, implicated in ~75% of threatened species (*18*). Increasingly well documented studies (*19*) show that habitat destruction is continuing and perhaps accelerating. Some now-common species will lose their habitats within decades.

Interestingly, accidentally or deliberately introduced species are blamed for only 6% of currently threatened birds (*18*). Yet introduced species, and the predation, competition, disease, and habitat modification they cause, are the most frequently cited factors in all the extinction centers we discussed above (*12*). Undoubtedly, many species will be lost to introduced species in ways that we cannot now anticipate. For example, no one considered the birds on the island of Guam to be in danger 30 years ago, but an introduced snake has eliminated all the island's birds since then (*14*). Were this predator to reach Hawaiʻi, all its birds would be at risk.

Calibrating Species Loss from Habitat Loss: A Tale of Two Forests

So far, we have sampled well-known, but disparate species whose high extinction rates probably typify the unknown majority. We now consider a typical mechanism of extinction: habitat loss. Can we predict species losses from estimates of habitat losses? The function $S = cA^z$ relates the number of species counted (S) to the area surveyed (A); c and z are constants (*20*). If the original habitat area, A_o, is reduced to A_n, we expect the original number of species, S_o, to decline eventually to S_n. Now $S_n/S_o = cA_n^z/cA_o^z$ or $(A_n/A_o)^z$— an expression that is independent of c. Across different situations, z varies from 0.1 to 1.0, but it is often taken to be $\sim$¼ (*20*). This value is typical of islands isolated by sea-level changes, a process that may be the best model for large habitat fragments isolated by deforestation (*20, 21*).

This recipe forms the basis of the predictions of 1000 to 10,000 *E*/MSY shown in Fig. 2. To challenge these estimates, critics point to the few bird extinctions after the clearing of North America's eastern forests (*3*). Is the recipe flawed? Only if interpreted naïvely are these results a poor model for what happens elsewhere.

An extinction "cold spot." European colonists cut >95% of the eastern forests of North America, but not simultaneously. Locally, forests reclaimed abandoned fields, and regionally forests recovered in the Northeast as settlers moved westward. Of the region's 2.87×10^6 km^2 area, forests always covered >50% (*21*). So 16% (= $0.5^{0.25}$)—or 26 of the ~160 forest species—should have gone extinct. Only 4 did so (*21*). Yet, such predictions are naïve. Not enough time may have elapsed for the extinctions to occur. However, all but 28 of these species occur widely across North America. They would have survived elsewhere even if all the forest had been permanently cleared. The cookie-cutter model restricts the analysis to the region's 28 endemics, whence the predicted and observed number of extinctions correspond (4 ≈ 16% of 28).

Simply, this region has very few endemics and so few species to lose. In contrast, tropical moist forests may hold two-thirds of all species on Earth (*22*). Despite inevitable differences in their definition, satellite imaging yields detailed and rapidly changing estimates showing their rapid depletion (*19*). The forests' global extent is variously estimated at 8×10^6 to 12.8×10^6 km^2 and their rate of clearing as 1.2×10^6 to 1.4×10^6 km^2 per decade (*19*).

An extinction "hot spot." The 1.47×10^6 km^2 of forests in the Philippines and Indonesia (excluding Irian Jaya) hold 545 endemic bird species—20 times the number in America's eastern forest in half the area (*23*). Only 0.91×10^6 km^2 of forest remains, and ~10% of the original area is cleared per decade. Using current satellite-based estimates of forest cover, the species-area recipe adequately predicts the number of species endemic to single islands that are currently threatened (Fig. 3A). The recipe, however, overestimates the numbers of currently threatened species that are found on several islands (Fig. 3B) and greatly overestimates the number of currently threatened species that are widespread (Fig. 3C).

Estimates of extinctions from habitat losses (Fig. 2) use an area's total number of species, not its smaller number of endemics. Does this reliance on such totals inflate these rates? In general, it does not, because many tropical areas are unusually rich in endemics (*13*). For example, 18 areas worldwide are so rich in endemics as to encompass ~20% of the known species of flowering plants in a total area of 0.74×10^6 km^2 (*16*). A larger area than this was cleared from the eastern American forests in the 19th century. The fate of these areas obviously dominates the calculations of future extinction rates. Details of land use changes in these areas are critical, but the details are not sufficient in themselves. We also need the detailed patterns of endemism.

Unfortunately, we know the geographical ranges of only a small proportion of the already small proportion of species for which we have names. We do have a comprehensive understanding of the geographical patterns of species richness (*20*). Its lessons are not encouraging. First, we cannot extrapolate from one species group to the next. For instance, across a continent species richness in frogs may not correlate with the species richness in birds (*24*). Worse, the direction of the correlation—positive or negative—may differ between continents (*24*). Second, areas rich in species are not always rich in endemics (*24*). Simply, our understanding of endemism is insufficient for us to know the future of biodiversity with precision (*25*).

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Restoring Value to the World's Degraded Lands

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Roughly 43 percent of Earth's terrestrial vegetated surface has diminished capacity to supply benefits to humanity because of recent, direct impacts of land use. This represents an ~10 percent reduction in potential direct instrumental value (PDIV), defined as the potential to yield direct benefits such as agricultural, forestry, industrial, and medicinal products. If present trends continue, the global loss of PDIV could reach ~20 percent by 2020. From a biophysical perspective, recovery of ~5 percent of PDIV is feasible over the next 25 years. Capitalizing on natural recovery mechanisms is urgently needed to prevent further irreversible degradation and to retain the multiple values of productive land.

Rehabilitation of the world's degraded lands is important for several reasons. First, increasing crop yields is crucial to meeting the needs of the growing human population (*1*) for food, feed, biomass energy, fiber, and timber (in the absence of a massive increase in the equity of global resource distribution (*2*). Second, anthropogenic changes in land productivity have deleterious impacts on major biogeochemical cycles that regulate greenhouse gas fluxes and determine Earth's total energy balance (*3*). Third, biodiversity preservation depends, in part, on increasing yields on human-dominated land to alleviate pressure to convert remaining natural habitat (*4*). And fourth, land is frequently a limiting factor of economic output, and its degradation threatens to undermine economic development in poor nations (*5*, *6*) and social stability globally (*7*).

Here I estimate the rate at which potential direct instrumental value (PDIV) could be restored to degraded lands from a biophysical (as opposed to socioeconomic) perspective. PDIV is the capacity of land to supply humanity with direct benefits only, such as agricultural, forestry, industrial, and medicinal products. It does not incorporate indirect values [for example, ecosystem services (*8*)], option values, or nonuse values (*9*) and is thus a conservative measure of value. PDIV is not the same as potential net primary production (NPP), and may even vary inversely with it; for example, average NPP in agricultural systems is typically lower (and DIV higher) than in the natural systems they replace (*10*). Because PDIV depends on complex and variable factors such as human knowledge and preferences,

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