

GLOBAL STATE OF BIODIVERSITY AND LOSS

Rodolfo Dirzo¹ and Peter H. Raven²

¹*Instituto de Ecología, Departamento Ecología Evolutiva, Universidad Nacional Autónoma de México, Mexico DF 04510; email: urania@ecologia.unam.mx*

²*Missouri Botanical Garden, St. Louis, Missouri 63166-0299; email: praven@nas.edu*

Key Words biodiversity hotspots, endemism, extinction, species diversity, species threatening

■ **Abstract** Biodiversity, a central component of Earth's life support systems, is directly relevant to human societies. We examine the dimensions and nature of the Earth's terrestrial biodiversity and review the scientific facts concerning the rate of loss of biodiversity and the drivers of this loss. The estimate for the total number of species of eukaryotic organisms possible lies in the 5–15 million range, with a best guess of ~7 million. Species diversity is unevenly distributed; the highest concentrations are in tropical ecosystems. Endemisms are concentrated in a few hotspots, which are in turn seriously threatened by habitat destruction—the most prominent driver of biodiversity loss. For the past 300 years, recorded extinctions for a few groups of organisms reveal rates of extinction at least several hundred times the rate expected on the basis of the geological record. The loss of biodiversity is the only truly irreversible global environmental change the Earth faces today.

CONTENTS

INTRODUCTION	138
THE FACETS OF BIODIVERSITY	138
BIODIVERSITY THROUGH TIME	140
GLOBAL MAGNITUDE OF BIODIVERSITY	141
Species Diversity	141
Intraspecific (Genetic) Diversity	142
Endemism	144
Domesticated Biodiversity	146
Biodiversity Novelties	147
ECO-GEOGRAPHIC DISTRIBUTION	148
The Distribution of Species, Families, and Orders	148
Population and Genetic Diversity Distribution	150
Distribution of Endemism	151
LOSS OF BIODIVERSITY	152
Prehistoric and Recent Extinctions	152
Threatened Species: How Many, Where, and Why	156
Current and Future Rates of Extinction	161

Threats to Populations	162
EPILOGUE	163

INTRODUCTION

Biodiversity—the sum total of all of the plants, animals, fungi, and microorganisms on Earth; their genetic and phenotypic variation; and the communities and ecosystems of which they are a part—is more rich and varied now than ever before (1), but it is threatened with a major pulse of extinction to which some authors have referred as the sixth major extinction of the Phanerozoic Era (2). Even though there is no consensus as to the magnitude of biodiversity on Earth, it has clearly reached unprecedented diversity as a result of more than 3.5 billion years of organic evolution. At the same time, human domination of the planet is so extensive (3) that Crutzen (4) has gone so far as to refer to the present as “the Anthropocene Era” (4). It is obvious to most scientists that extinction is rampant at present, but a few skeptics have demurred, claiming that this is “a doomsday myth” (5) or that the estimates of extinction are “strident, inconsistent and data-free” (6).

In this paper we shall examine the dimensions and nature of the Earth’s terrestrial biodiversity and review the scientific facts concerning the rate of loss of this biodiversity and the factors that are causing this loss. This review is important because (a) biodiversity is a central component of Earth’s life support systems and directly relevant to human societies; (b) any attempt to defend a social cause, such as biodiversity, should rest on the best facts available; and (c) the loss of biodiversity is the only truly irreversible global environmental change the Earth faces today. We shall concern ourselves solely with eukaryotic organisms, because the facts are not yet available to support a comparable discussion of prokaryotic diversity.

THE FACETS OF BIODIVERSITY

The standard definition of biodiversity implies a logical link between the three levels it comprises: The organisms that make up a population of a given species behave and respond to their environment as they do as a result of the features determined by their genetic constitution. Species are constituents of communities that, with their physical environment, form the ecosystems, landscapes, and ultimately biomes.

Other facets of biodiversity are important from a functional and evolutionary point of view. These include the diversity of functional groups (or, in the case of plants, life forms); the proportion of endemic taxa; and the diversity of cultivated and domesticated species and their wild relatives. Life forms reflect the adaptive ways in which organisms respond to the selective pressures of the environment; in turn, the relative composition of life forms is reflected in the “spectra” characterizing a given kind of ecosystem (7). Such a classification helps also to define the

structure and diversity of communities; an additional aspect of this approach is that it can facilitate comparisons between whole communities and their environments. For example, plant life form diversity in a tropical rain forest would include several species of herbs, epiphytic herbs, shrubs, hemiepiphytic trees, light-demanding and shade-tolerant trees, vines, lianas, palms, and parasitic plants; different types of forest will have contrasting relative abundances of each life form (8).

The proportion of taxa in a specified geographical area that is found nowhere else constitutes an important qualitative aspect of biodiversity—endemism. Initially, scientific interest in endemism was related to biogeographical and evolutionary studies, but currently an appreciation of endemism facilitates the formulation of conservation strategies worldwide. Endemism can be expressed at different levels; thus species, genera, families, orders or even phyla can be endemic to a given region. In a different sense, regions may have endemic life forms, as is the case of seasonally dry tropical forests of Madagascar, the Namib Desert, or Mexico, in which succulent and other unusual plants of bizarre form abound.

Domestication, the process by which plants and animals are selected from wild populations and adapted to special environments created by humans, is another important facet of biodiversity. Even though cultivated and domesticated plants and animals represent a very small fraction of the total species (see below), they constitute almost all of the food we consume and are thus of great importance (9).

Finally, another salient aspect of biodiversity is the occurrence, in some regions, of distinct biotic elements of different biogeographic origins in the same area. This includes the mingling of boreal temperate and Neotropical or Madrean elements, for example the co-occurrence of taxa of Nearctic and Neotropical origin in Mexico/Central America, or the confluence of animals and plants from the Indomalaysian and Australasian regions in the islands between Java and New Guinea. Such meeting grounds of biogeographic provinces are reflected in unique assemblages of organisms including, for example, communities of boreal trees such as oaks, *Liquidambar*, and walnuts with austral *Cecropia*, *Nectandra*, and tree ferns in a small area in southeast Mexico and monkeys, marsupials, and cockatoos with other Asian and Australasian birds on a single tree in Indonesia (10).

Most analyses of biodiversity have been carried out at the level of species, even though the relationships both at higher taxonomic levels and genetic variation within species are also of great interest. Frequently in this paper, as in the literature generally, we shall use “biodiversity” to refer to species-level patterns of distribution.

In dealing with species diversity, the number of species per unit area or locality, one measure of the biological richness of a region, is termed alpha diversity. In contrast, beta diversity is a measure of the changes in species composition from one area to an adjacent one. If we speak comparatively of all the species in a given region, such as tropical America, or biome, such as the short-grass prairies of North America, we use the term gamma diversity. Thus a latitudinal gradient of higher tropical than temperate diversity of birds or plants is due to higher levels of alpha, beta, and gamma diversity.

BIODIVERSITY THROUGH TIME

Figure 1 shows the time-course of biological diversity throughout the Phanerozoic Period, the last 600 million years of life on Earth. The figure also shows the five major extinctions (arrows) that took place during this period.

Available fossil evidence suggests that diversity of families of multicellular marine organisms (Figure 1*a*) rose steadily through the Cambrian Period, attaining a plateau near the end of the Ordovician Period (about 440 million years ago) and then punctuated by a great wave of extinction in the Permian (290–245 million years ago), and subsequently increased steadily to the present. The trend in species number (not shown in Figure 1) is even more extreme: relatively low from the early Cambrian Period (some 540 million years ago) until the mid-Cretaceous Period, and then increasing tenfold over the past 100 million years (12). Terrestrial organisms first appeared about 440 million years ago, near the start of the Silurian Period, with the invasion of the land by the ancestors of plants, fungi, vertebrate animals, and arthropods—each group increasing rapidly in diversity from that time onward.

At the species level, vascular plants, an essentially terrestrial group, began to diversify markedly around 400 million years ago and declined during the worldwide Permian extinction event that also affected marine organisms profoundly (Figure 1*b*), and then began, like marine organisms, to diversify around the middle of the Cretaceous Period, some 100 million years ago, with the flowering plants (angiosperms) the dominant group thereafter.

The fossil records of both marine and terrestrial multicellular eukaryotes indicate maximum diversity at the present time (Figure 1). The present level of marine diversity is estimated to be about twice the average over the past 600 million years (12), and that of terrestrial diversity perhaps also about twice its historical average since organisms first invaded the land about 440 million years ago. The trend has been continually upward despite the five major extinction events that have occurred over the past 570 million years, which essentially covers the history of multicellular organisms (Figure 1). Nevertheless, this widely cited pattern of temporal increase in biodiversity through the Phanerozoic Era must be taken with caution. On the one hand, there is the “pull-of-the-recent effect” (13), whereby young rocks are more likely than old rocks to be well preserved, and thus the most recent occurrences of species are more likely to be found than the older occurrences. Moreover, a considerable fraction of the recent marine faunas are known from single rocks, from restricted localities. For example, Pliocene collections of macrofossils from the Isthmus of Panama constitute about 18% of the total Pliocene diversity, despite the fact that this area of Pliocene deposition is less than 0.1% of the 7 million km² of Pliocene deposition worldwide (14). It has been claimed that in order to accurately assess the trajectory of the increase in marine biodiversity during the Phanerozoic Period a comprehensive, global program directed to obtain new data is urgently needed (14).

The fossil record and the application of several analytical treatments to the data [largely the survivorship patterns of thousands of cohorts of fossil genera (15)]

suggest that the average species has a life span of $\sim 5\text{--}10$ million years, including a range from about 1 to 13 million years for mammals and planktonic foraminifera, respectively (2). If throughout their geological history species last $10^6\text{--}10^7$ years, it follows that their rate of extinction is 1–0.1 species per million species-years [see (16)]. However, because species longevities are based on the geological divisions in which they lived, species lifetimes may be overestimated while, conversely, records from single exposures of rock will lead to underestimates of species' true lifetimes. An important, independent source of information supports the million-year life span of species as a conservative estimate: molecular phylogenies that permit estimates of speciation rates (16). Since natural extinction rates cannot greatly exceed speciation rates, models in which lineages have the same probability of giving birth to a new lineage or going extinct allow the estimation of the rate parameters. The relevance of these estimates will become evident in our subsequent discussion of biodiversity loss.

GLOBAL MAGNITUDE OF BIODIVERSITY

Species Diversity

There are some 100 phyla of living organisms (17), but the total number of species they include is very poorly known. Complete catalogues of the described, valid species exist for only a few groups of organisms, and so the total can only be estimated; May (18) calculates it at 1.5 million species, lowering an earlier estimate by Hammond (9) at 1.75 million species. Much more difficult to estimate is the actual number of living eukaryotic species; moreover, methods of estimating the number and definition of prokaryotic species and viruses are still very limited, and we are omitting them from further consideration here. Relatively reliable estimates are available for some groups of vertebrate animals and some groups of plants and insects (e.g., butterflies and mosquitoes), but for others, especially nematodes, fungi, and mites, the estimates are much less certain—but the groups are certainly very large. Estimates of the total number of species of organisms are based on expert opinions by those who understand the level of diversity in a particular group of organisms well, extrapolations from an initial estimated number, or combinations of these methods. Thus sampling with an analysis of results has yielded estimates like Erwin's (19) of 30 million species of tropical arthropods based on the sampling of beetles in tropical tree canopies. The results of several of the expert opinions and extrapolations available are summarized by Pimm et al. (16). Such estimates deal essentially with possible orders of magnitude rather than actual numbers, leading to a fair degree of uncertainty [see (20)]. The number of described species typically falls 1–2 orders of magnitude below the extrapolated number, while expert opinions fall towards the middle of the range, and the extrapolated values move towards $10^6\text{--}10^8$. The most recent, comprehensive, and careful effort to estimate the number of species overall is that of May (18), who

reworked earlier estimates carefully from a statistical and factual point of view and effectively replaces Hammond's (9) earlier efforts in this area. May concludes that the best estimate for the total number of species of eukaryotic organisms possibly lies in the 5–15 million range, with a best guess of around 7 million species. Papers presented at a recent symposium (21) rework what can most logically be deduced about the number of species in individual groups and update the efforts of Hammond (9) in this regard.

Looking at the current rates of publication of new species [e.g., 13,000 animal species per year; see (9)], it is evident that the task of describing the total number of species on Earth will not be completed for many decades, even assuming they can all be collected and put into the hands of the appropriate experts. For flowering plants, Prance et al. (22), taking as their base the traditional estimate of 250,000 valid, described species, noting that an average of 2350 species had been described each year in the preceding nine-year period, and considering the rate of discovery of novelties throughout the world, estimated that perhaps 50,000 to 70,000 additional valid species remain to be described. Remarkably, recent estimates have strongly suggested that the assumption of 250,000 valid, described species may not be even approximately accurate! Thus, Bramwell (23), using the number of species of the largest country in a given region of the world as a "baseline flora" to which he added the number of local endemics from the other countries of that region, arrived at an estimated number of 421,968 species. This number is very similar to that suggested by Govaerts (24), 422,000, based on the enumerations presented in the first volumes of his *World Checklist of Seed Plants*. If these estimates are verified, then the total number of species of flowering plants could be as high as 500,000 or even more. A verified world checklist is urgently needed to provide an adequate baseline for knowledge about this extraordinarily important group of organisms.

Recent collections of papers and encyclopedias (21, 25, 26) present estimates of the total number of species either described or predicted for individual groups of organisms, and such efforts will and should continue as the base is made more secure. Despite all of the uncertainties, we can conclude with May (18) that the eukaryotic organisms can best be estimated as between 5 and 15 million but that it is still conceivable that the figure could be greatly increased, even by as much as an order of magnitude, by new discoveries (1, 16).

Intraspecific (Genetic) Diversity

In its broadest sense, genetic diversity embraces the diversity at all levels of an ecological or taxonomic hierarchy. Within species, this diversity exists at three levels: inside individuals, between individuals of a population, and between populations. Here we will stress variation within and between populations, the latter expressed as the relative proportion of the variation between and within populations, or population divergence. An enormous and only partly explored degree of genetic variation exists within populations.

A single, well-explored example will illustrate the richness and complexity of this variation. The following observations relate to plants of white clover (*Trifolium repens*), a stoloniferous perennial species, from a population growing in a 1-ha field in North Wales and analyzed for variation in those genes associated with different characters of known selective importance. Among 50 clones selected from the field, all but a few differed in the combinations of genes affecting their fitness in nature (27). For example, in a reciprocal transplant experiment, four different types of clover plants expressed differential competitive abilities depending on the neighboring grass species, each usually expressing its best performance when transplanted into conditions like those from which it originated (28). Another adaptive feature was marked by the occurrence of both cyanogenic and acyanogenic individuals, the former releasing cyanide when physically damaged by herbivores. Such individuals occurred in different parts of the field depending on the relative density of herbivores and thus the probability of being attacked (29). Furthermore, at least nine different morphs of leaf marks were found in different individuals (30); the character might be relevant in interactions with herbivores. Finally, several clover forms are known with different susceptibilities to being infected by nitrogen-fixing *Rhizobium* bacteria. These traits are mainly genetically determined, and even for the relatively few that we have mentioned here, the potential combinations of genetically distinct variants within this 1-ha field are very numerous. Comparable results have often been found for other species that have been investigated, and it is clear that the level of genetic diversity in out-crossing species generally is extremely large, as geneticists have demonstrated with increasing precision for populations of both plants and animals over the course of many decades.

Many species are composed of populations that are genetically more or less distinct from one another. A well-known example is the case of ecotypic differentiation, which has been demonstrated within many plant species over nearly a century [e.g., (31)]. Such differentiation occurs in relation to gradients in physical habitats, and it is widespread both in plants and in animals, sometimes even over short distances and relatively brief periods of time. A classic example here is the differentiation of plants that have invaded tailings from abandoned mines (32). In general, the more extensively such studies are conducted, the more variation is encountered.

What is the magnitude of population diversity at a global scale? The answer to this seemingly unmanageable question was attempted by Hughes et al. (33) by analyzing information on Mendelian populations of eukaryotic species. They first estimated the average number of populations per unit area from the literature on population differentiation [a total of 81 publications, including vertebrates (35), plants (23), arthropods (19), and one flatworm]. This estimate yielded a value of one population per 10,000 km² for an average species. To estimate the approximate average number of populations per species, they calculated the average range size per species from published range maps. The estimated value was 2.6 million km² (but they used the average for butterflies, 2.2 million km², as it was considered more conservative). The number of populations per unit area and the average range size

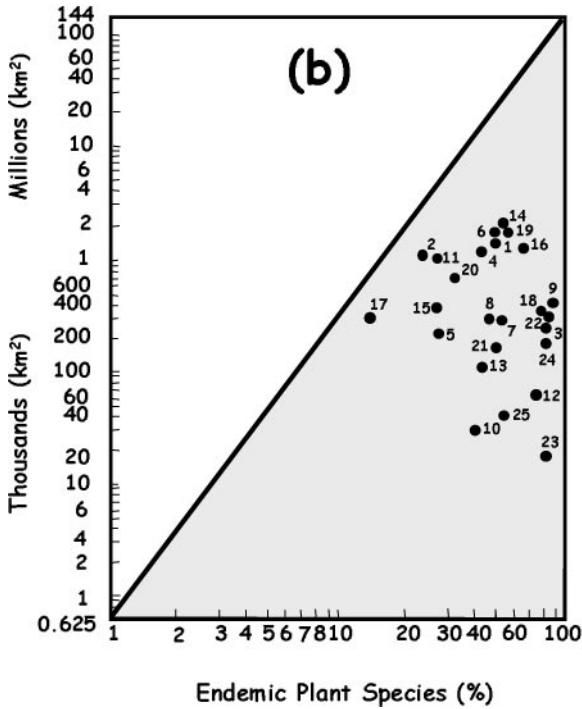
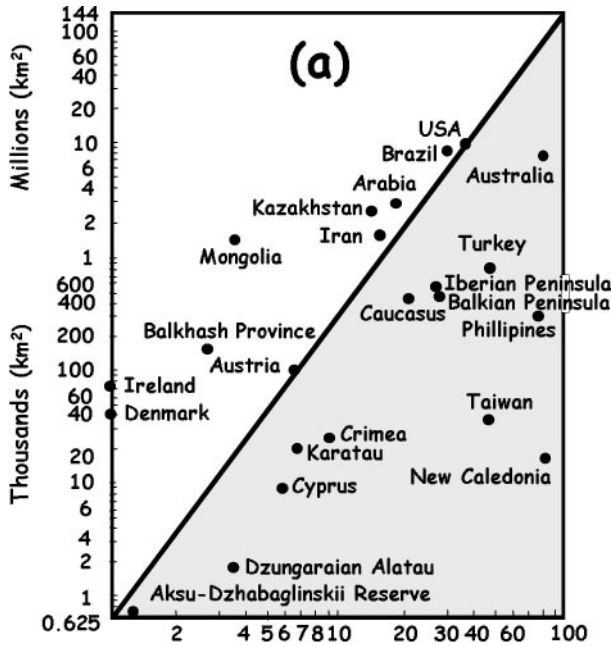
were combined to estimate the number of populations per species, and this yielded a value of 220 (i.e., $2.2 \times 10^6/1 \times 10^4$). This value, multiplied by the presumed number of species on Earth, should give a global estimate. For the global species number, they used three values: 5, 14, and 30 million, and the corresponding populations were 1.1, 3.1, and 6.1 billion globally. Although very tentative, these estimates certainly illustrate the point that population diversity at the global scale is enormous. They also form a rough reference estimate for our subsequent discussion of the potential magnitude of biodiversity loss at the population level.

Endemism

Endemism refers to the restriction of kinds of organisms to particular geographical areas, with many different factors responsible for its nature and extent. In an interesting general analysis, Bykov [1979, 1983, cited in (34)] described the relationship between plant species endemism and area across a range of spatial scales, up to the size of the global, total land area. The magnitude of endemism of an area increases with size of that area. Given that the totality of all vascular plants is endemic to the total land area of earth, at this area the level of plant endemism is 100%, and should be lower for any smaller area. Bykov suggests that the lowest endemism for a “concrete” flora (i.e., one not truncated in number by the sample area being too small) should be 1%, which, he suggests, occurs at an area of 625 km², a size consistent with other minimum data points discussed by Major (34). This data point and that for the land area of the Earth (and its total flora) define a straight line on a log-log plot of percent endemism and area (Figure 2*a*). The precise size of the area at 1% endemism is arbitrary, but Bykov notes that the slope of the relationship is little influenced by changes in endemism values in the range 300 km² to a few thousand km².

Bykov’s plot gives us a qualitative and quantitative means of assessing the relative degree of endemism for a given locality. Qualitatively, localities lying above the line will have less than normal endemism; those below will have more, a useful point of reference. One can observe that the degree of endemism for the United States or Austria lie approximately on the line, whereas some small

Figure 2 Bykov’s plant endemism plot [cited in (34)] showing (a) the relationship between percentage of endemic plant species in different floras and their corresponding area. The diagonal runs across a minimum of 1% endemic plant species and its corresponding area to the total number of plant species endemic to the Earth in the total surface land area; and (b) the location of Myers’ et al. (35) hotspots of global biodiversity on Bykov’s plant endemism plot. The 25 hotspots were plotted on the basis of data on percent endemism and their original area obtained from Myers et al. For identification of the 25 hotspots see (35). The shaded areas in both plots show the domain of endemism-rich regions. Figure modified from the original plot by Bykov, with permission.



countries such as Denmark or Ireland, depauperate in endemics, lie on the Y-axis, at a height of around the $50 \times 10^3 \text{ km}^2$ tick. Areas that lie below the line, and particularly those located in the smallest possible quadrats in the lowest-right area of the plot, are the most endemic-rich. For example, New Caledonia has 68% endemic species in an area of $18.3 \times 10^3 \text{ km}^2$. Quantitatively, Bykov defined an index of endemism l_e , on the basis of the degree of departure of our site of interest, E_i , from the global expected, normal value read off the line, E_n , as $l_e = E_i/E_n$. One then has to look for values greater or lower than 1.0 for sites with endemism levels greater or lower than the global normal, respectively. Biodiversity “hotspots” [see (35)], in terms of their degree of endemism, would be placed largely toward the plot’s lower right sector. We shall discuss them further below.

Domesticated Biodiversity

About a third (173) of the more than 500 families of flowering plants have one or more crop species (9)—amounting to a total of about 2500 species overall. The grass family (Poaceae) has the largest number (379) and is closely followed by legumes, Fabaceae, with 337; the two families together include about 30% of all crop species. Ten more families (Apiaceae, Arecaceae, Asteraceae, Brassicaceae, Chenopodiaceae, Menthaceae, Rosaceae, Rutaceae, Solanaceae, and Zingiberaceae) have from a few to many dozens of crop species each, with the numerous other families including only one or a few species. Among the roughly 2500 crop species, just 103 supply over 90% of the calories humans consume, directly or indirectly (36), with just three grasses (cereals), rice, wheat, and maize, supplying over 60% of the total. More than 15 plants are cultivated as sources of fiber, and thousands more as ornamentals or sources of medicines. (Perhaps a tenth of the total species, more than 25,000 plant species overall, are or have been used as sources of medicines, but the great majority of these are collected directly from nature.)

Most crops are genetically diverse, as evidenced by the many land races that exist in the major cereals and such crops as bananas, cassava, potatoes, and tomatoes. Distinctive variants are also characteristic of many crops; for example, cabbage, cauliflowers, broccoli, kohlrabi, Brussels sprouts, calabrese, and kale are all selected variants of *Brassica oleracea*.

Of the approximately 50,000 described vertebrate species 30–40 species of birds and mammals have been domesticated. Apart from dogs and cats, four species of domestic mammals have a global distribution (except for the Antarctic) and are impressively dominant numerically: cattle (1300 million), sheep (1200 million), pigs (850 million), and chickens (10 billion) (9). Most of the remaining domesticated animal species are more limited, like those of the Andean camelids (llamas and vicuñas). As in domesticated crops, the degree of infraspecific variation in animals is astonishing: for example, there are about 800 distinct breeds each of cattle and sheep. Although the vast majority of the domesticated animals are used as food, they also provide wool, tallow, bone, manure for fuel and fertilizer, and leather, and they are used very widely as draft animals.

Biodiversity Novelties

With perhaps one in ten species of the Earth's eukaryotic organisms having been discovered, it should not be surprising that strikingly novel and wholly unexpected new taxa should continue to be discovered among the 15,000 to 20,000 new species that are annually described. Even for relatively well-known areas like the United States, the rate of discovery suggests that no more than a third to a half of the estimated total 500,000 to 750,000 species of organisms have yet been discovered. For flowering plants, perhaps 1000 new species await discovery in addition to the 18,000 already known to this country (37).

The number of new species has been rising over the past decade to levels comparable to those of the mid-eighteenth to late nineteenth century (38). Much of this discovery, as for mammals, seems to be directly correlated with serious exploration of new areas. Thus, fieldwork over the last decade in the Annamite mountains on the border of central Vietnam and Laos has brought to light a new bovid and at least three new species of muntjac deer, together with what seems to be a new genus of rabbit (39). Similar trends have been demonstrated for other groups of vertebrates (38).

Some of the new discoveries are of evident economic importance, such as a species of maize, *Zea diploperennis*, from the state of Jalisco in western Mexico, which is interfertile with cultivated maize but unique in its perennial habit; it is restricted to a disturbed area about the size of a football field and was discovered only 25 years ago (40).

Even a few new phyla and classes of eukaryotic organisms are being found each decade, mostly from marine habitats. The continued exploration of southern Mexico and Central America has led to the discovery of two new families of plants during the past two decades, one of them (Ticondendraceae) a locally fairly abundant tree species (41) and the other (Lacandoniaceae) comprising a slender, parasitic, achlorophyllous root-parasite, with a unique floral structure in which the pistillate organs surround the staminate ones (42). Occurring at a single locality in Chiapas, the latter plant is in danger of extinction. Other remarkable botanical examples, all newly discovered palms from Madagascar [narrated by Prance et al. in (22)], include the smallest palm (less than 27 cm in height), *Dypsis tenuissima*; an aquatic palm, *Ravenea musicalis*, with fruit and seeds with adaptations for flotation and aquatic dispersal and known only from a single population of about 450 plants along a river; and *Satranala* sp. nov. with a peculiar, hard endocarp that features flanges unlike those of any other palm endocarp, which may have facilitated the dispersal of its seeds by the recently extinct giant elephant bird.

Additional bizarre discoveries include many organisms, catalogued by Donoghue and Alverson (38), with unique life styles: an agaric fungus that fruits under the ice of lakes in far southern South America; an Australian frog that raises its tadpoles in its stomach; and a Brazilian caecilian that is three times the length (up to 0.8 m) of the largest lungless amphibian previously known. Most striking among the terrestrial invertebrates is the recent report of a new order of the class insecta from the Afrotropics (43)! This new order, the Mantophasmatodea, is

represented by insects that look like a cross between a cricket and a stick insect, and it is the first of this taxonomic hierarchy to be discovered for more than 80 years. Once it was discovered in the field in Namibia, museum specimens collected over a period of more than a century were recognized from other parts of southern Africa. And the list goes on and on! Clearly we live in an age of discovery; one in which the geographic exploration of rapidly dwindling natural areas, coupled with increasingly deep phylogenetic analyses, is revealing much that has been unsuspected about the nature of life on Earth.

ECO-GEOGRAPHIC DISTRIBUTION

Many trends in the distributional patterns of biodiversity are well established. The most evident of these is that of species diversity, which increases from high to low latitudes in most groups that have been well analyzed. We show here that the distribution of higher taxonomic categories as well as other aspects of biodiversity tend to follow the same geographic gradient and review other additional eco-geographic trends as well. A comprehensive discussion of the causal factors underlying such gradients is, however, out of the scope of this paper.

The Distribution of Species, Families, and Orders

We begin with the interesting exercise carried out by Williams et al. (44). These authors combined the available data about the distribution of families for plants, amphibians, reptiles, and mammals using three combinatory approaches: summing the absolute family richness, the proportional family richness, and the proportional family richness weighted for the presumed total species richness of each family. The diversity of the groups for these parameters was mapped onto a cylindrical equal-area projection of the world, using equal-area grid cells of 10^0 . The three approaches yielded similar results, which showed a consistent gradient of richness from high to low latitudes. In addition, the Americas were consistently richer than the Old World. The area of maximum family diversity was northern South America for two of the three analyses, with that for weighted family diversity being Central America. Kaufman (45) demonstrated a similar gradient for mammalian orders in the New World.

Latitudinal variation in species richness has been estimated in many different ways, including various arbitrary units of area, and these have yielded comparable gradients for the groups considered, with low latitudes in general richer in species than higher ones [see reviews in (1, 25, 26, 46)]. It also seems to apply to the fossil record, at least for the past 70 million years or so [see Figure 2.23 in (1) for fossil Foraminifera].

There are so many examples of studies of this kind that we selected only a few to review here—ones that illustrate the general principles. Global maps often show species richness of different taxa plotted as a world density surface. In the case of plants, for example, a map has been constructed based on ca. 1400 literature

records from different geographic units with mapped richness values calculated on a standard area of 10,000 km² using a single species/area curve (47). The map in Figure 3 shows the Americas. Superimposed on this map we present plant species density data for specific localities sampled by A. Gentry (48). This remarkable data set corresponds to a large number of sites for which local species diversity of trees with a minimum diameter at breast height of 2.5 cm was enumerated at the scale of 0.1 ha with a highly standardized protocol and extremely high-quality species identification. In addition, we applied regression analysis of latitude with species diversity for the Gentry data. The three analyses show a very consistent latitudinal gradient of plant diversity. In broad geographic terms, species densities range from over 5000 species/10,000 km² in tropical regions to less than 100 in the highest latitudes. In terms of local species diversity values range from an average of 270 species per 0.1 ha in Colombia to ca. 15 near the U.S.-Canadian border. In addition, the relationship between latitude and local species diversity from the Gentry data was highly significant ($F = 33.1$; $P < 0.0001$; $R^2 = 0.56$). Furthermore, Figure 3 makes evident the occurrence of high-diversity centers, including western Amazonia, Brazil's Atlantic Coast, and Mesoamerica.

Similar analyses have been performed for other continents, and the overall results are consistent with those of Figure 3. Species density maps are also available for other groups [see (11) and <http://stort.unep-wcmc.org>]. For the botanical example just presented, data were not available to explore to what extent the latitudinal gradient is explained by species turnover. However, a recent study (49), comparing species composition among 20 tropical dry forest sites in Mexico, showed that 72% of a total of 917 sampled species were present only in a single site and that the average similarity (Sorensen's index) among sites was only 9%. Such a high species turnover in tropical sites has been found in other studies of plants and for vertebrates as well, as we discuss below.

Our final example concerns the distribution patterns of mammals (45). The species richness of mammals (excluding bats) for natural communities in the New World shows the same overall latitudinal gradient that we have mentioned for plants. In addition, an analysis of species turnover among localities showed that beta diversity was also higher at lower latitudes. These analyses indicate that the regional increase of species richness towards the equator (i.e., gamma diversity), appears to be a consequence of great increases both in local species richness (alpha diversity) and in species differentiation among communities (beta diversity).

Species number analyses of plants suggest that about 90,000 species, approximately twice as many as in Africa south of the Sahara, occur in the Neotropics and that the comparable area of Asia is roughly intermediate in this respect. This, then, is the same relationship as shown in the family analysis for plants and vertebrates presented above. Fogging sampling techniques using standardized protocols yield comparable data for canopy beetles (species/m³) and the results have the same tendency (although the values are even more contrasting than in the case of plants): 1.17 in Panama and 1.15 in Peru >0.29 in New Guinea >0.02 in Australia and Sulawesi. Similar tendencies have been observed in numerous other groups,

including butterflies (Neotropics > Southeast Asia > Africa), frogs (Neotropics > Africa/Asia > Papua/Australia), and birds (Neotropics > Africa > Asia/Pacific > Australopapuan). In mammals, the number depends on the particular group (bats: Neotropical > Old World; primates: Old World > New World). It should be stressed, however, that many groups of eukaryotic organisms (e.g., nematodes, fungi, and mites) are so poorly known that we cannot at present state with confidence that they will, when better known, exhibit similar latitudinal or longitudinal patterns of species richness.

Our acceptance of the generality of the latitudinal gradient discussed above deserves two cautionary comments. On the one hand, there are a number of notable exceptions to the peak near the equator pattern, including ichneumonid wasps, shorebirds, penguins, and salamanders [see (26) for a discussion of these and additional examples], all of which have their diversity peaks at higher latitudes. Furthermore, as we noted earlier, we do not actually know enough about many groups to be sure whether their species would display a latitudinal gradient or, if they did, in which direction it may run. On the other hand, a very important determinant of the observed geographic patterns of species distribution, including the latitudinal gradient, is the “mid-domain effect” (50)—referring to the geometry of species ranges in relation to geographical boundaries. The principle of this effect is that species with wide ranges, when randomly placed within a bounded geographical domain, will tend to pile up in the middle (e.g., near the equator), while species with small ranges can, by chance alone, be anywhere. Such geometric models explain a significant proportion of the empirical variation in latitudinal richness for some wide-ranging taxa. The geographic patterns of narrow-ranging taxa, less constrained by geometry, are more likely to reflect local environmental and historical factors, and in the absence of a compelling theory of endemism, we will continue to be unable to understand why some groups of organisms sometimes match expected patterns of geographic distribution and sometimes do not.

Population and Genetic Diversity Distribution

The data concerning global variation in genetic diversity are extremely limited, but the few available studies suggest that, again, there is a significant latitudinal trend. On the one hand, evidence on genetic variation measured by allozyme diversity across phylogeny shows that genetic diversity varies nonrandomly among populations, species, and higher taxa and also among ecological parameters, including habitat type and climatic region. With regard to eco-geographic variation, a global study of 1111 species, analyzed for allozymic variation (an average of 23 loci per species) and 21 independent variables associated to them (51), found that ecological factors account for the highest proportion of the explained genetic variance among species, as compared with demographic and life history factors. The study shows that mean heterozygosity decreased in the direction tropical > temperate > arctic life zones. Higher genetic diversity, as far as our limited results to date allow us to extrapolate to the general pattern, characterizes species typical of tropical regions.

On the other hand, domesticated biodiversity provides insights related to genetic diversity and its geographic distribution. Simply, the location where the origination of crops and of agricultural development occurred provides a view of the distribution of this facet of biodiversity. The major crops have their centers of genetic diversity in geo-economically defined developing countries/regions, largely in the Neotropics, Middle East, the Mediterranean and Northern Africa region, East Africa, South and Southeast Asia, and China. Many of the countries with higher concentrations of species diversity are located in tropical regions, which also coincide with the location of many of the centers of origin and development of major crops, see (10).

Distribution of Endemism

Endemic taxa are very unevenly distributed across the Earth. The available literature makes evident the existence of significant centers of endemism both at regional and global scales and for a variety of taxa (52). Considering the absolute number of endemic species, we find a negative correlation with latitude for species richness in general (52), but the percentage of endemism may be lower at low latitudes. In addition, there are many exceptions to these general trends; for example, the percentages of endemics and often the absolute number are higher on islands and in areas of Mediterranean climate than they are elsewhere.

Centers of endemism (53) tend to be concentrated at lower latitudes in the Southern Hemisphere (where the continental masses are much more widely separated than in the North) and on islands. Myers et al. (35), elaborating on their earlier studies, presented centers of endemism as "hotspots" and defined them on the basis of their concentration of endemic plant (and to some extent vertebrate) species and the degree of threat to the long-term survival of natural habitats in the areas they selected. For an area to qualify as a hotspot, it must include a minimum of 1500 endemic plant species (equivalent to 0.6% of the 250,000 described species estimated to have been named at that time), and no more than 30% of its original vegetation remains. The 25 selected areas show a considerable congruence between the degree of endemism of plants and vertebrates. We carried out Spearman rank correlation analyses between percent plant endemism and plant and vertebrate species diversity, as well as percent endemic vertebrates, and in all cases the relationship was highly significant (plants: $r_s = 0.79$, $P < 0.0001$; vertebrates: $r_s = 0.49$, $P = 0.012$; percent endemic vertebrates $r_s = 0.63$; $P = 0.0007$). These remarkable areas contain an estimated 133,149 endemic plant species (44% of all plant species) and 9645 endemic vertebrate species (35% of the total) in an area of just 1.4% of the Earth's total. Not surprisingly, when we plot the position of the hotspots in Bykov's graph (Figure 2b), all 25 of them fall below the line of normal, globally expected levels of plant endemism. Only two of them fall relatively close but below the line because they have levels of endemism below 25%. While the 25 hotspots feature a variety of ecosystem types, the predominant ones are tropical moist forests, 15, and Mediterranean ecosystems, 5; 9 consist partly or completely of islands, and 16 are in the tropics at large.

In a recent analysis (54), the evolutionary history of two groups of mammals (primates and carnivores) residing in the hotspots was estimated by considering two measures: clade evolutionary history (the branch length within a clade in a phylogeny of the two groups) and species evolutionary history (the branch length from the present to the time of divergence for the species). The analysis indicated that, collectively, about 70% of the total evolutionary history of these two groups is found within the 25 hotspots. Thus not only 55% of the world's primates and 22% of the world's carnivores are endemic to the hotspots, but a large proportion of the evolutionary history of the two groups resides there.

The latitudinal gradient, the megadiversity countries, the centers of endemism, and the hotspots are all manifestations of the fact that global biodiversity is highly concentrated in a few patches of the Earth. Certainly the tropics, and particularly tropical moist forests, stand out as highly significant reservoirs of global biodiversity. Not surprisingly, the world's records for local biodiversity come from the tropics, particularly the moist tropics: 1200 species of beetle from a single tree species (19), 365 tree species in a 1-ha plot (55) or 365 plant species in a 0.1-ha plot, considering the contribution of non-tree plants (56) and, overall, an estimated half of the global species richness in just 6% to 7% of the land.

LOSS OF BIODIVERSITY

Prehistoric and Recent Extinctions

As we have seen, nature is patchy, plentiful, and beautiful. However such biological wealth is seriously threatened by human activities, and the threat is even more serious than it might appear at first. Next we review this extraordinarily important problem.

Extinction is the ultimate fate of all species. As we discussed earlier, given the known species life span, we can infer that the species currently living amount to only 2% to 3% of those that have ever lived (2). We also know that five significant extinction events occurred during the Phanerozoic Era (Figure 1), but because a lower number of species were present at all times in the past, these events collectively seem to have ended no more than 5% to 10% of the species that ever lived. The species at risk now represent an unusually high proportion of all those that ever lived.

Historically, it appears that a recent pulse of extinction started during the late Quaternary Period (57), intensified about 40,000 years ago, and apparently has not ended. An excellent summary of this is in Lovei (58), from which we sketch the salient points.

During the Wisconsin glaciation (ending ca. 10,000 years ago), about 71% of mammalian genera from mid-latitude North America were lost. Many of these lived through cycles of glacial-interglacial periods, with general conditions at their worst during the period prior to the extinctions. Indeed, conditions had improved

at the time when most extinctions took place. The postglacial extinctions appear to be connected to the appearance of human beings in the affected areas. In addition to the mammals, 19 genera of large birds, mostly raptors, disappeared at this time. It is possible that the loss of mammals cascaded up to raptors, as happens in Africa when ungulate populations are reduced. In Australia, many species went extinct during the late Pleistocene, including all 19 marsupials heavier than 100 kg, most of the species of 10–100 kg body weight, three reptiles, an ostrich-sized bird, and an additional bestiary including tens of other large species. Recent evidence using refined radiocarbon dating (58) suggests that human predation is the probable cause of these Australian extinctions. The evidence for human-induced defaunation in Africa is limited and clearly needs additional study. Nevertheless, the coincidence of human presence (and the evidence of human proficiency at hunting) in North America and Australia with the selective loss of large animals, in what is geologically and evolutionarily a very short period, strongly suggests the causal role of humans in this wave of extinctions. Of the three hypotheses proposed to explain the megafaunal extinctions of this period, kill (overhunting), chill (low temperatures), and ill (pathogenic disease), overhunting seems to be the most consistent one (57–58a).

In addition, the extinction of many species on islands during the last 10,000 years is clearly correlated with the arrival of humans there (the so-called “first contact extinctions”). The examples are numerous. In Madagascar, massive extinctions started to take place soon after the arrival of human beings. Seven of the 17 primate genera have gone, while two more have lost their larger species, most of which were probably diurnal. Among the birds, extinction was significant for large-bodied, flightless species—the elephant birds. To this list we can add the pigmy hippo, the endemic aardvark, and two giant land tortoises, among others.

Before the arrival of humans in New Zealand, apart from two species of bats, there were no terrestrial mammals. In the absence of predators, birds, many of them flightless, prospered. There were two kinds of ratite birds, moas and kiwis. The dozen species of moas, with body sizes ranging from some 25 kg to 250 kg, were all exterminated as a consequence of intensive hunting by the Maori people as well, probably, as land clearing. In addition, the activities of the Maori were apparently responsible for the loss of a number of species of flightless, ground nesting, diurnal bird species, and a predator of the moas, the giant eagle (*Harpagornis moorei*), was lost along with its prey.

The colonization by humans of the Pacific Islands eastward and northeastward from southern Asia resulted in the elimination of some 1000 species of birds over a period of about 1000 years in this area alone—about a tenth of the world total that existed before the Polynesian colonizing voyages took place. Studies of these islands suggest that about half the species present when humans arrived have been preserved as fossils and that they and about an equal number of unknown species were lost as a result of human activities (59). For those bird species that have survived on Pacific islands, the future does not appear bright. Thus, of the

estimated 125–145 nonmarine bird species that once lived in Hawaii, 27 have survived, but only 11 are abundant enough that their survival does not appear questionable.

The evidence that we have just reviewed indicates that a massive extinction event, driven by human beings, has been underway for some 40,000 years. In recent times, when we have more exact estimates of extinction, the situation has become far more drastic, as reviewed recently by the World Conservation Union (IUCN) (60), which we use as the basis of our review from the year 1500 A.D. onward. The total recorded extinctions for this 500-year period are 811 species, including 331 vertebrates, 388 invertebrates, and 92 plants. Figure 4 shows the proportional distribution among major groups for vertebrates, invertebrates, and plants. Among the vertebrates, the highest proportion is that of birds, followed by fish and mammals. Among the invertebrates, the largest contribution is due to terrestrial and freshwater mollusks, with 308 extinct species, the greatest total for any group for this period. In addition, 4 marine mollusks are known to have become extinct during this period. The figures for plants are too manifestly incomplete to form a useful basis for analysis.

In addition to these numbers, the 2002 IUCN list permits exploration of the changes in recorded extinctions between 1996 and 2002. During this seven-year period, the number of recorded vertebrate extinctions increased by 16 species and mollusks by 69 species, mostly because of increased exploration and taxonomic clarification within the United States.

A geographical analysis of the 811 recorded extinctions since 1500 shows that the occurrence is not random. Most have taken place on islands, although some studies suggest that the percentage of threat in continental areas may be underestimated (61); these calculations should be taken seriously in planning conservation strategies for the future. The statistics themselves must be viewed in the perspective of the very strict criteria employed by the IUCN for accepting that a species is extinct; for example, several hundred species of plants are considered extinct in current floras, but for one reason or another have not been listed by the IUCN. Examples include Goldblatt and Manning (62), who consider 36 plant species extinct in the Cape Floristic Province of South Africa, and the common understanding that well over 50 plant species have become extinct in Hawaii during the past two centuries (P.H. Raven, unpublished data). Whatever the true number, it would, since only a very few groups of organisms are well enough known to be assessed for extinction, clearly be only a very small fraction of the total species that have become extinct during that period of time. For tropical moist forests, some 19 of each 20 species would be unknown to science at present so the effects of burning forests of this kind result in a catastrophe beyond imagination.

What is clear is that extinction rates for the past several hundred years have been at least several hundred times historical values (63). The fact that we have documented so few extinctions does not mean that they are not happening. A compelling analysis (64) shows that sampling biases lead to artificially low estimates of extinction and threat in poorly studied taxa. In this analysis a positive and

Recorded Extinctions (811)

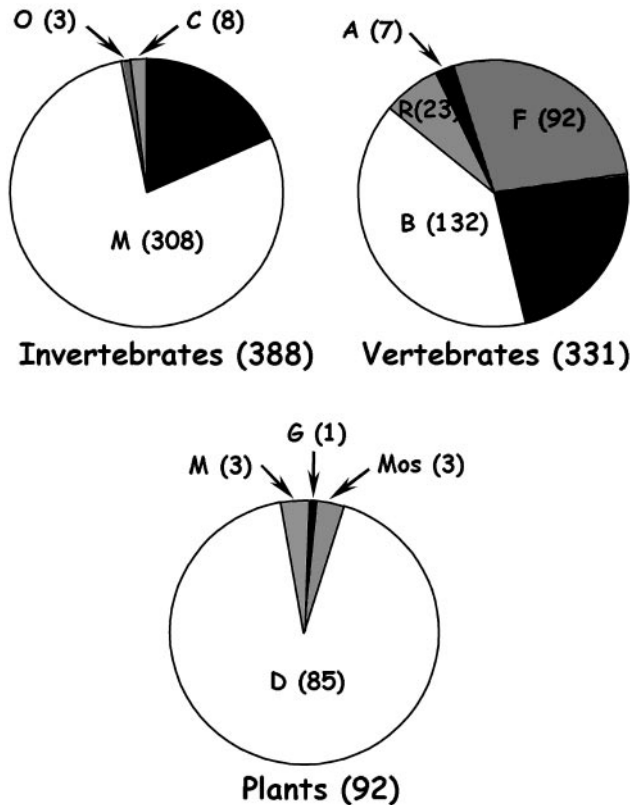


Figure 4 Percentages (actual numbers are in parentheses) of recorded extinct species of vertebrates, invertebrates, and plants since 1500. The symbols used in the figure for vertebrates are: M, mammals; B, birds; R, reptiles; A, amphibians; F, fish. The symbols used for invertebrates are: I, insects; M, mollusks; C, crustaceans; O, onychophorans. Plant symbols are: M, mosses; G, gymnosperms; D, dicotyledons; Mo, monocotyledons. Derived from data in (60).

significant relationship was found between the magnitude of knowledge (defined by the percentage of recorded species) of several groups and the percentage of threatened and extinct species in such groups: The more under studied a group is, the more likely we are to miss extinctions of all but the most abundant and visible species. The groups that we know well enough to produce such estimates are diverse both in their life histories and in their geographical distributions. They

are clearly typical of the many groups of organisms about which we know too little to make estimates of extinction. With widespread habitat destruction, increasingly adverse impact of alien invasive species, and overexploitation, there is no doubt that the rate of extinction will climb rapidly during the century we have just entered. We can gauge this by looking at the magnitude of threat and its geographic distribution.

Threatened Species: How Many, Where, and Why

The most comprehensive list of globally threatened species is the IUCN 2002 edition of threatened species (60). This list includes 11,167 threatened species (Figure 5) facing a high risk of extinction in at least the near future resulting both directly and indirectly from human activities. Although this is a small number relative to the total number of species (i.e., less than 1%), it includes 24% and 12% of all mammals and birds, respectively. The corresponding values for the other vertebrates are lower but still high if one considers the numbers as a proportion of

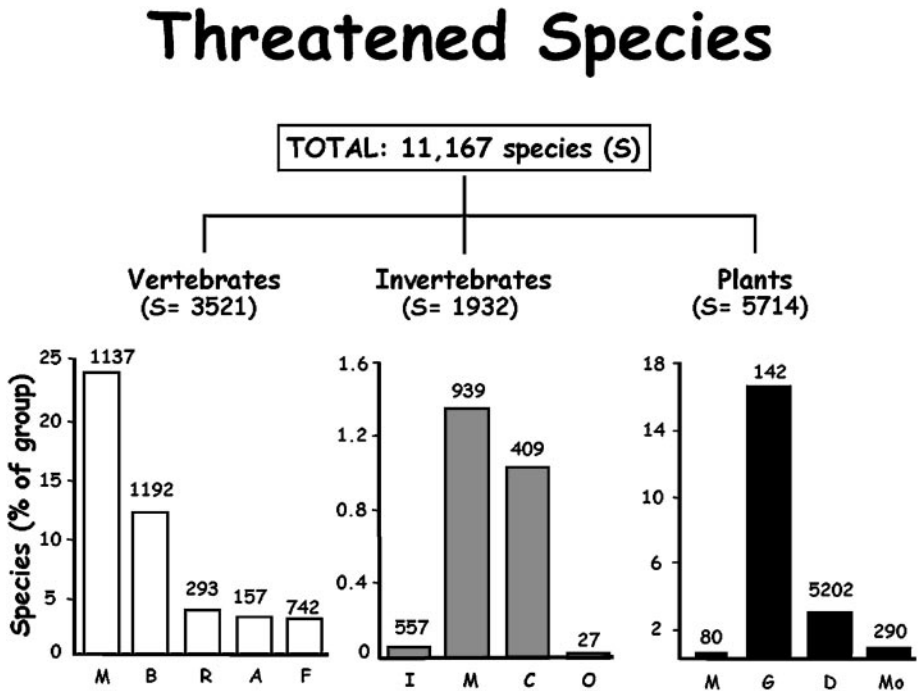


Figure 5 Percentages (and number) of threatened species of vertebrates, invertebrates, and plants in year 2002. The symbols used in the figure for vertebrates are: M, mammals; B, birds; R, reptiles; A, amphibians; F, fish. The symbols used for invertebrates are: I, insects; M, mollusks; C, crustaceans; O, others. Plant symbols are: M, mosses; G, gymnosperms; D, dicotyledons; Mo, monocotyledons. Derived with permission from data in (60).

the number of species actually evaluated, in which case about 25% of the reptiles, 21% of the amphibians, and 30% of the freshwater fish are threatened. Using very strict criteria, this would lead to a conclusion that approximately 20% of all vertebrates may actually be threatened at the present time. The real figure may very well be much higher. For invertebrates, only a few species have been evaluated and the statistics are too few to allow reasonable extrapolation.

For plants, the IUCN number represents only 2% to 3% of the known species, but that is clearly a serious underestimate. For gymnosperms, which are the only comprehensively assessed group, the value is 16%. Looking at individual countries, Master et al. (65) estimated that ca. 33% of the plant species native to the United States are threatened with extinction, including 24% of the conifers. Because the U.S. assessment also suggests that 14% of the birds and 16% of the mammals are threatened, figures relatively close to the IUCN world totals, they indicate that threatened plants are seriously underrepresented in the global figures. Freshwater species are the most seriously threatened in the United States with 37% of the fish, 69% of the freshwater mussels, and 51% of the crayfish considered to be in this status.

The 2002 IUCN report presents the data for animal species threatened in 1996 as well, and thus estimates can be made of the changes in the categories of threat among them. We calculated the proportional changes in the number of species in three categories of threat between 1996 and 2002 (Table 1). The salient aspects of this analysis are that proportional increases are considerable in the critically endangered and endangered categories. In the former, increases are particularly high in amphibians (a 66.7% increase, from 18 species in 1996 to 30 species in 2002) and reptiles, and in the latter the same occurs with birds, reptiles, and amphibians. There are two interesting decreases, mollusks in the critically endangered category and birds in the vulnerable category. In the former case, the explanation is that

TABLE 1 Percentage changes in the numbers of species of seven groups of animals in three categories of threat. The values were calculated as the proportional difference of the numbers recorded in each category in 1996 and 2002. Derived with permission from (60)

Group	Critically endangered	Endangered	Vulnerable
Mammals	7.1	7.6	0.8
Birds	8.3	38.7	-2.8
Reptiles	34.1	33.9	3.9
Amphibians	66.7	19.4	20.0
Fish	0	6.7	-0.2
Insects	4.5	1.7	4.2
Mollusks	-13.6	11.3	6.7

several of the mollusks in this category have been shown to become extinct, and in the birds of the 24 species that decreased, some were removed from it, but others moved to higher categories of threat. In sum, some of the changes resulted from new additions, but many were changes in status as a result of increasing threats; in particular, the situation of birds appears to be deteriorating.

The threats to biodiversity are not homogeneously distributed; the 2000 IUCN report (60a) allows for distinguishable patterns to be discerned with regard to geography and ecological (e.g., biome) affinity, among other things. Thus a large majority of the threatened mammal species occurs in tropical countries. The top of the list is Indonesia, with 135 species, followed by India, Brazil, China, and Mexico. As a percentage of the total number of mammal species in each country, the ranking of the top countries changes, but the majority of the countries, 8 out of the top 10, are still tropical. The significant outliers of a regression, between the total number of species versus threatened species, in all assessed countries constitute a group of nations that have more threatened species than expected. Of the 25 outliers, 19 are island states, but the group includes mainland countries such as India, Brazil, China, Bhutan, and Vietnam. This highlights the patchy nature of threats to biodiversity and a significant concentration in some tropical and island states. For birds, again, in absolute numbers, most of the countries with a high number of threatened species are tropical, Indonesia leading again with 115 species, closely followed by Brazil with 113. Here, the ranking changes notably when percentages of threatened species in faunas of particular countries are used. In this case, New Zealand is at the top of the list with 42% of its birds threatened, followed by the Philippines with 35%. The outliers of the regression analysis of species and endemism per country, again, include 15 island states and 10 continental nations in the tropics (Brazil, India, Colombia, Peru, and Ecuador; the most significant outliers) and outside the tropics (China and the Russian Federation). The United States is another outlier, but this is largely due to the situation in Hawaii and other islands that are included.

In the case of plants, the 1997 IUCN red list reports an overall figure of 13% species threatened. The numbers in the 2002 IUCN report have serious limitations as indicated above but, again, the tropical-insular predominance is evident: Malaysia has an extremely large number, 681 species, followed by Indonesia, 384; Brazil, 338; and Sri Lanka, 280; but it is clear that many factors have caused these assessments to be uneven. Some countries such as South Africa (60) and the United States (63) are clearly underrepresented, as are many poorly known tropical areas.

Recently, a new approach has been proposed to estimate global degree of endangerment for plants (66). This approach attempts to overcome the lack of information for tropical plants by considering that the number of plant species endemic to a country is a good proxy for the number that are threatened. For one well-studied tropical country, Ecuador, the authors estimate that approximately 83% of the endemic plant species qualify as threatened by the IUCN criteria. Because data on tropical endemism are better than for degree of threat, the use of such information and land area for 189 countries/regions led to five different estimates

of global threat. The range of estimates (intended to take into consideration the effect of several potentially misleading factors, such as the fact that species endemic to small countries are more likely to be threatened than species endemic to large countries) varied from 22% to 47%. The latter figure results if the number of known species of flowering plants is estimated at 250,000, and the former if recent estimates of approximately 420,000 (reviewed above) are correct. Perhaps, then, a reasonable interim estimate would be that a third of the plant species of the world are threatened. This estimate, suggested against a background of inadequate knowledge, is extremely worrying considering our absolute dependency on plants and the many ways in which we expect to use them for our benefit in the future.

Considering that species with small ranges (i.e., endemic) are more apt to be threatened than those more widely distributed (16, 67), in the context of our lack of knowledge of many groups of organisms, 33% might be a reasonable estimate of the proportion of the world's biota that are threatened with extinction as we enter the twenty-first century. Such figures are likely to be higher for islands generally and also for Latin America, South Africa, and South and Southeast Asia, for reasons that we discussed earlier. Tropical forests of all kinds, with their very high concentrations of species, rapidly increasing human populations, rising expectations for living standards, and the globalization of the economy, are under particular threat.

We turn now to the question of drivers of extinction, which can be divided into two categories: proximal and ultimate. A revision of the ultimate drivers is outside the scope of this paper, but we refer to a synthetic statement of Ehrlich & Kremen (68). They refer to the $I = PAT$ equation: impact of the human enterprise on nature is the product of population, affluence (per capita consumption), and technology. The three variables causing the impact have to do with population growth, i.e., overconsumption, poorly designed environmental technologies, and faulty economic arrangements (for example, the fact that market prices of several resources do not reflect the real social costs). Biological extinction is ultimately rooted in these social, economic, and political drivers that, accordingly, require ultimate solutions from the social domains. To organize appropriate action, however, we also need relevant information on the nature, extent, and distribution of the proximal drivers, which we briefly review next.

The 2000 IUCN (60a) report analyzes the causes of threat to a sample of 720 mammalian threatened species, 1173 threatened birds, and 2274 plants. This survey shows that habitat loss/degradation is the most important threat to the three groups, affecting, respectively, 89%, 83%, and 91% of the sampled threatened mammals, birds, and plants. Specifically the primary causes of habitat loss are agricultural activities (including crop and livestock farming and plantations), extraction activities (mining, fishing, logging, and harvesting), and the development of infrastructure (such as human settlements, industry, roads, dams, and power lines). Of these specific drivers, agricultural activities affect 827 (70%) of the threatened species of birds, 1121 (49%) of the plant species, and apparently only 92 (13%) of the threatened species of mammals. Extraction has its greatest impact

on plants, affecting 1365 (34%) species, but 622 bird species (53%) were also affected. Developmental activities affect 769 threatened plant species and 373 bird species, but only 59 (8%) of the threatened mammals. The low number of mammal species apparently affected by these drivers may reflect lack of information, and 495 mammal species (69%) were placed in this category. Studies at more local levels, for example in tropical forests of southeast Mexico (69), show that forest fragmentation is the leading cause for the local extinction of several mammal species with medium or large body size. Given the high concentration of threatened species in tropical ecosystems, and given the fact that tropical forests are clearly an endangered ecosystem because of deforestation, increasing utilization for various human activities, and fragmentation [see (70)], we can expect a tremendously high risk of extinction due to tropical deforestation.

The driver second in importance in the IUCN assessment is direct exploitation. The threats to 37%, 34%, and 8% of the sampled bird, mammal, and plant species arise from hunting, trading, and collecting. At a regional scale, hunting is particularly critical for mammals, especially in the tropics. It was estimated that subsistence hunting alone may be responsible for the killing of ca. 14 million animals per year in the Brazilian Amazon (71), and the problem is a very well known driver of extinction in Africa and Asia also.

Third in importance in the IUCN study is the introduction of alien invasive species of plants and animals, which affects 350 species (30%) of all threatened birds and 361 (15%) of the plants, but only 69 (10%) of the mammals. It is clear that this driver is especially serious for birds. In fact, a majority of the contemporary, since 1800, extinctions of birds, particularly on islands, can logically be attributed to the activities of introduced animals. Currently, it is estimated that virtually all (100%) of the threatened species on Hawaii are in danger of extinction because of the activities of introduced plants and animals. For the mainland United States, between 25% and 40% of the threats to extinction for native plants stem from the activities of introduced alien invasive plants and animals. In fact, it is likely that on a world scale, the introduction of alien invasive species is second only to habitat destruction as a source of extinction for plants and animals—a clear indication that conservation organizations and other bodies concerned with ameliorating threats to extinction need to deal with this problem much more seriously than has been traditional.

We now return to our discussion of the hotspots. As we have seen, in the scheme of Myers et al. (35), a hotspot has to have at least 1500 endemic plant species and only 30% of remaining natural habitat. Twenty-five such hotspots were identified (see Figure 2). Although collectively they covered 12% of the global land area, an average of seven eighths of their natural vegetation has been destroyed, so that the relatively natural areas in them now comprise only about 1.4% of the world's total land. Because taken together they contain nearly half of the world's plants and a third of all terrestrial vertebrates, they represent areas of enormous threat to a major proportion of the world's remaining biodiversity and, at the same time, afford hugely significant opportunities for conservation. Habitat loss within

the original hotspots has doubtless already driven many thousands of species, most of them unknown, to extinction with many more at threat now (72). They, along with oceanic islands, bodies of fresh water, and the tropics in general are especially critical to the survival of a major proportion of the existing biodiversity on Earth. In all of these areas, the huge and growing threats posed by introduced invasive alien species already present and potentially arriving in the future deserve much closer attention than they have received in the past as a major element in the depauperization of the world's endowment of biodiversity—our common heritage.

Current and Future Rates of Extinction

The background rate of species extinction over the past 65 million years has, as we have seen, amounted to 0.1–1 species per million species per year or less [see (16, 63)]. These estimates, based on information reviewed above, provide a yardstick for measuring current and projected future rates of extinction.

Over the last few thousand years humans have eliminated an estimated 10% of the world's species of birds. In some local instances, extinctions have reached more than 90%. This is documented information, not predictions. A thorough review of recorded extinction rates for vertebrates, plants, and some other groups of organisms for the past 300 years has revealed rates of extinction at least several hundred times the rate expected on the basis of the geological record (63). Such rates are particularly high for species with limited ranges, low local abundances, and geographic concentration in areas that are being changed rapidly.

The loss of habitat is the predominant driver of threat and extinction, so that principles that relate area loss and extinction/threat can operate as a useful tool to investigate current risk. These can be calibrated with known numbers of threatened/extinct species available for some places. This raises the question of how much area is necessary to conserve how many species.

Because habitat loss is the principal driver of extinction throughout the world, the survival times of species in small remaining areas of habitat should be considered in relation to their likely time of survival: How long does it take to lose species under such circumstances? The species (S)-area (A) relationship that has been shown to be valid for areas of similar habitat throughout the world is described by the power function $S = cA^z$, where c is a constant and z is the slope of the relationship. The slope, z , has typical values of about 0.15 for increasingly larger areas within a continuous habitat and higher ones, more like 0.25, for comparisons between actual islands in an archipelago. Because of this relationship, observations of habitat loss permit the prediction of the number of species that are likely to survive. For areas that have long been partly deforested, such as North America (73) where no more than a third of the total area of the eastern temperate forests survived at any one time in the past, the model predicts the loss of 4 species of birds, which is the actual number of bird species extinct or on the brink of extinction in the region. In contrast, in areas of recent deforestation, insular

Southeast Asia (74) and Brazil's Atlantic forest (75), the model adequately predicts the number of bird species threatened with extinction in the medium term.

For these cases we need to estimate how long it takes to lose species in fragmented habitats. The use of the species-area relationship permits estimates of the number of species in the pre-fragmentation stage and the number that will become extinct after fragmentation. These, together with a survey of the current species surviving in the fragmented habitat, permit in turn estimates of a "relaxation index," the ratio of the proportion of extinctions yet to occur after time t (e.g., years), to the proportion that will eventually occur. Such an index will equal 1.0 immediately after fragmentation and will eventually decline to zero. Assuming that the decline in species is exponential, we can characterize it by a fixed time to lose half its species, the "species half-life." An empirical study of these predictions in fragments of the Kakamega forests of western Kenya (76) calculated life times of birds to range between 25 and 75 years, 50 years on the average. This means that of the contingent of species the fragments are going to lose, they will lose half in about 50 years, and about three quarters of them in a century.

We can now put the findings of these studies and our knowledge of threats together to get a global picture of extinction. In the case of birds, the current number of threatened species is 1192, largely due to habitat loss and fragmentation. To use conservative and round numbers, we can predict that at least 500 (but probably closer to 600) of them will go extinct in the next 50 years, yielding an extinction rate of over 1000 extinctions per million species per year—some 1000 times higher than the background rate of 1.0. Using the same half-life of 50 years, we can predict that some 565 of the 1137 threatened species of mammals will go extinct within the next 50 years due to habitat loss and fragmentation. The corresponding prediction of the relative rate using again a conservative value of 500 (instead of 565) produces an extinction rate of over 1000 species per million species per year. Similar exercises using the values of Figure 5 yield a panorama of widespread extinctions in fragmented habitats within a period of some five decades, again, with extinction rates 2+ orders of magnitude higher than background rates.

Threats to Populations

Undoubtedly, a major pulse of extinction has already occurred, is currently taking place, and will continue to occur at the population level. Estimates of species extinction/threat will underestimate such intraspecific extinctions. No data are available to document these massive biological extinctions. Hughes et al. (33) proposed that we may assume a populations-area relationship in a one-to-one (linear) pattern, as opposed to a typical species-area relationship under the $S = cA^z$ model. This is due to a question of size: a population occupies a small area, relative to a species. In this way, when a large amount of area is destroyed, several populations may go extinct while few species are likely to be lost, because other populations of the species exist elsewhere, and the rate of population extinction will be faster than that of species extinction. For example, with a slope (the z value) of

0.30, a habitat loss of 90% will commit 50% of the species to extinction, while 90% of the populations in the original habitat will be lost. Hughes et al. (33) did a thought experiment assuming an annual tropical deforestation of 0.8%, a global population diversity of 3 billion (two thirds of which exist in tropical regions), and calculated an extinction rate of 16 million populations per year. These calculations may be debatable, yet their message is obvious: a major pulse of biological extinction is and will be taking place at the population level. For example, a study of 173 mammalian species on six continents shows that, collectively, these species have lost over 50% of the areas of their historic ranges, especially in regions where human activities are intense (77).

EPILOGUE

The described current patterns of biodiversity distribution and extinction and its drivers underscore the urgent need to protect habitats, particularly habitats rich in species and particularly those rich in endemic species. The 1994 IUCN assessment of protected areas (78) shows a rather gloomy perspective. The assessment indicates that 8641 protected areas in categories I–V (those with low/no human intervention) existed, covering an area of 7.9 million km², equivalent to 5.3% of the Earth's surface. However, only 3.7% were in categories I–III, those with the best conservation potential. In addition, the frequency distribution of park sizes is strongly right-skewed, with most of them of small area and only a few large ones. Although a 5.3% area of habitat may imply a rough potential for conservation of 50% of the global species diversity (on the basis of the species-area relationship), a closer look at the regional distribution of protected areas shows that the percentage ranges from 0.3 to 10.9 with the highest values in North America (10.9%), Europe (9.1%), and Australia (10.6%), while many of the critical biodiversity areas have lower values. In addition, many parks in general only exist as “paper parks” without an effective and comprehensive protective scheme in place.

The regions used in the 1994 IUCN assessment are artificial. From an ecological standpoint, it is of great importance that the rate of creation of protected areas in tropical forests peaked in the 1980s, and has tended to fall since. It is therefore doubtful that more than 10% of the tropical forests will be protected, and probably more realistic to think of 5% surviving the next 50 years. Such a reduction in the area of these forests would lead, ultimately, to the extinction of perhaps three quarters of the species living in the forests originally with no more than 1 in 10 of the species ever having been discovered or described scientifically. The restoration of deforested or damaged areas will have a very beneficial effect on the survival of many of the species that may be hanging on in fragments of forest now. At any event, more than a third of the existing species on Earth could disappear with the destruction of the tropical forests.

Considering the wider threats to species in other tropical areas, on islands, and in nontropical hotspots because of alien invasive plants and animals that are spreading

rapidly over the face of the globe and the selective hunting or gathering of wild species, it is reasonable, although pessimistic, to envision the loss of two thirds of the species on Earth by the end of the twenty-first century—an incalculable loss for the Earth and for humanity and the prosperous, sustainable future of mankind. We must do what we can to prevent such a loss, to limit it, by the most careful planning of which we are capable and the appropriate allocation of resources worldwide. The dimensions of the sixth great extinction are still matters of human choice, and millions of species that otherwise could be lost during the course of this century can be saved by decisive and appropriate actions, well considered and taken as soon as possible.

ACKNOWLEDGMENTS

We are grateful to Stuart L. Pimm for his enthusiastic and valuable help in all stages of the preparation of this review, including constructive comments on previous drafts. We thank Guillermina Gómez, Arturo Dirzo, Laura Zenteno, and Raúl I. Martínez for their help in the preparation of figures and literature search.

**The Annual Review of Environment and Resources is online at
<http://environ.annualreviews.org>**

LITERATURE CITED

1. Rozensweig ML. 1995. *Species Diversity in Space and Time*. Cambridge, GB: Cambridge Univ. Press
2. May RM, Lawton JH, Stork NE. 1995. Assessing extinction rates. In *Extinction Rates*, ed. JH Lawton, RM May, pp. 1–24. Oxford: Oxford Univ. Press
3. Vitousek P, Mooney HA, Lubchenco J, Melillo JL. 1997. Human domination of Earth's ecosystems. *Science* 277:494–99
4. Crutzen PJ. 2002. Geology of mankind. *Nature* 415:23
5. Budiansky S. 1993. The doomsday myths. *US News World Rep.* Dec. 13:81–83
6. Mann CC, Plummer ML. 1995. *Noah's Choice*. New York: Knopf
7. Raunkiaer C. 1934. *The Life Forms of Plants*. Oxford: Oxford Univ. Press
8. Dirzo R. 2001. Tropical forests. In *Global Biodiversity in a Changing Environment. Scenarios for the 21st Century*, ed. FS Chapin, OE Sala, E Huber-Sannwald, pp. 251–276. New York: Springer
9. Hammond PM. 1995. Magnitude and distribution of biodiversity. In *Global Biodiversity Assessment*, ed. VH Heywood. Cambridge, GB: Cambridge Univ. Press
10. Sarukhán J, Dirzo R. 2001. Biodiversity-rich countries. See Ref. 26, 1:419–36
11. Groombridge B, Jenkins MD. 2002. *Global Biodiversity: Earth's Living Resources in the 21st Century*. Cambridge, GB: World Conserv. See also <http://stort.unep-wcmc.org>
12. Sepkoski JJ Jr. 1992. Phylogenetic and ecologic patterns in the Phanerozoic history of marine biodiversity. In *Systematics, Ecology, and the Biodiversity Crisis*, ed. N Eldridge, pp. 77–100. New York: Columbia Univ. Press
13. Raup DM. 1972. Taxonomic diversity during the Phanerozoic. *Science* 177:1065–71
14. Jackson JBC, Johnson KG. 2001. Measuring past biodiversity. *Science* 293:2401–04

15. Raup DM. 1978. Cohort analysis of generic survivorship. *Paleobiology* 4:1–15
16. Pimm SL, Russell GJ, Gittleman JL, Brooks TM. 1995. The future of biodiversity. *Science* 269:347–50
17. Margulis L, Schwartz KV. 1998. *Five Kingdoms, An Illustrated Guide to the Phyla of Life on Earth*. New York: Freeman
18. May RM. 2000. The dimensions of life on Earth. In *Nature and Human Society: The Quest for a Sustainable World*, ed. PH Raven, T Williams, pp. 30–45. Washington, DC: Natl. Acad.
19. Erwin TL. 1982. Tropical forests: their richness in Coleopteran and other arthropod species. *Coleopt. Bull.* 36:74–75
20. Gaston KJ. 1991. The magnitude of global insect species richness. *Conserv. Biol.* 5:283–96
21. Raven PH, Williams T, eds. 2000. *Nature and Human Society: The Quest for a Sustainable World*. Washington, DC: Natl. Acad.
22. Prance GT, Beetle H, Grandfield J, Johns R. 2000. The tropical flora remains undercollected. *Ann. Missouri Bot. Gard.* 87:67–71
23. Bramwell D. 2002. How many plant species are there? *Plant Talk* 28:32–34
24. Govaerts R. 2001. How many species of seed plants are there? *Taxon* 50:1085–90
25. Heywood VH, ed. 1995. *Global Biodiversity Assessment*. Cambridge, GB: Cambridge Univ. Press
26. Levin SA, ed. 2001. *Encyclopedia of Biodiversity*. San Diego: Academic. 5 Vols.
27. Burdon JJ. 1980. Intraspecific diversity in a natural population of *Trifolium repens*. *J. Ecol.* 68:717–35
28. Turkington R, Harper JL. 1979. The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. IV. Fine scale biotic differentiation. *J. Ecol.* 67:245–54
29. Dirzo R, Harper JL. 1982. Experimental studies on slug-plant interactions. IV. The performance of cyanogenic and acyanogenic morphs of *Trifolium repens* in the field. *J. Ecol.* 70:119–38
30. Cahn M, Harper JL. 1976. The biology of the leaf mark polymorphism in *Trifolium repens* L. I. Distribution of phenotypes at a local scale. *Heredity* 37:309–25
31. Turesson G. 1922. The genotypical response of the plant species to the habitat. *Hereditas* 6:147–236
32. Antonovics J, Bradshaw AD. 1970. Evolution in closely adjacent populations. VIII. Clinal patterns at a mine boundary. *Heredity* 25:349–62
33. Hughes JB, Daily GC, Ehrlich PR. 1997. Population diversity: its extent and extinction. *Science* 278:689–91
34. Major J. 1988. Endemism. A botanical perspective. In *Analytical Biogeography. An Integrated Approach to the Study of Plant and Animal Distributions*, ed. AA Myers, PS Giller, pp. 117–46. New York: Chapman & Hall
35. Myers N, Mittermeier RA, Mittermeier C, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–58
36. Prescott-Allen R, Prescott-Allen C. 1990. How many plants feed the world? *Conserv. Biol.* 4:365–74
37. Ertter B. 2000. Floristic surprises in North America North of Mexico. *Ann. Missouri Bot. Gard.* 87:81–109
38. Donoghue MJ, Alverson WS. 2000. A new age of discovery. *Ann. Missouri Bot. Gard.* 87:110–26
39. Ginsberg JR. 2001. Biodiversity of mammals. See Ref. 26, 3:777–810
40. Iltis HH, Doebley JF, Guzmán R, Pazy B. 1979. *Zea diploperennis* (Graminae): a new teosinte from México. *Science* 203:186–88
41. Gómez-Laurito J, Gómez LD. 1989. *Tico-dendron*: a new tree from Central America. *Ann. Missouri Bot. Gard.* 76:1148–51
42. Martínez E. 1989. Lacandoniaceae (Triuridales): una nueva familia de México. *Ann. Missouri Bot. Gard.* 76:128–35
43. Klass KD, Zompro O, Kristensen NP, Adis

- J. 2002. Mantophasmatodea: a new insect order with extant members from the Afrotropics. *Science* 296:1456–59
44. Williams PH, Gaston KJ, Humphries CJ. 1997. Mapping biodiversity value worldwide: combining higher-taxon richness from different groups. *Proc. R. Soc. Lond. B.* 264:141–48
45. Kaufman DM. 1995. Diversity of New World mammals: universality of the latitudinal gradients and bauplans. *J. Mammal.* 76:322–34
46. Willig MR. 2001. Latitude, common trends within. See Ref. 26, 3:701–14
47. Barthlott W, Biedinger N, Braun G, Feig F, Kier G, Mutke J. 1999. Terminological and methodological aspects of the mapping and analysis of global biodiversity. *Acta Bot. Fennica* 162:103–10. See also <http://www.botanik.uni-bonn.de/system/biomaps.htm#worldmap>
48. Phillips O, Miller JS. 2002. *Global Patterns of Plant Diversity: Alwyn H. Gentry's Forest Transect Data Set*. St. Louis, MO: Missouri Bot. Gard.
49. Trejo R, Dirzo R. 2002. Floristic diversity of Mexican seasonally dry tropical forests. *Biodivers. Conserv.* 11:2063–48
50. Colwell RK, Lees DC. 2000. The mid-domain effect: geometric constraints on the geography of species richness. *TREE* 15:70–76
51. Nevo E. 2001. Genetic diversity. See Ref. 26, 3:195–213
52. Cowling R. 2001. Endemism. See Ref. 26, 2:497–507
53. Bibby CJ, Crosby MJ, Johnson TH, Long AJ, Sathersfield AJ, Thirgood SJ. 1992. *Putting Biodiversity on the Map: Global Priorities for Conservation*. Cambridge, GB: Int. Counc. Bird Preserv.
54. Sechrest W, Brooks TM, Fonseca GAB, Konstant WR, Mittermeier RA, et al. 2002. Hotspots and the conservation of evolutionary history. *Proc. Natl. Acad. Sci. USA* 99(4):2067–71
55. Valencia R, Valslev H, Paz y Miño GC. 1994. High tree alpha-diversity in Amazonian Ecuador. *Biodivers. Conserv.* 3:21–28
56. Gentry AH, Dodson CH. 1987. Contribution of nontrees to species richness of a tropical rain forest. *Biotropica* 19:149–56
57. Martin PS, Klein RG, eds. 1984. *Quaternary Extinctions: A Prehistoric Revolution*. Tucson: Univ. Ariz. Press
58. Lövei GL. 2001. Modern examples of extinctions. See Ref. 26, 2:731–43
- 58a. Alroy J. 2001. A multi-species overkill simulation of the end-Pleistocene megafaunal extinction. *Science* 292:1893–96
59. Pimm SL, Moulton MP, Justice LJ. 1994. Bird extinctions in the Central Pacific. *Phil. Trans. R. Soc. London Ser. B* 344:27–33
60. Hilton-Taylor C. 2002. *IUCN Red List of Threatened Species*. <http://www.redlist.org>
- 60a. Hilton-Taylor C. 2000. *IUCN Red List of Threatened Species*. World Conserv. Union, Gland Switzerland
61. Manne LL, Brooks TM, Pimm SL. 1999. Relative risk of extinction of passerine birds on continents and islands. *Nature* 399:258–61
62. Goldblat P, Manning JC. 2002. Plant diversity in the Cape Region of southern Africa. *Ann. Missouri Bot. Gard.* 89:281–302
63. Pimm SL, Brooks TM. 2000. The sixth extinction: how large, where and when? In *Nature and Human Society: The Quest for a Sustainable World*, ed. PH Raven, T Williams, pp. 46–62. Washington, DC: Natl. Acad.
64. McKinney ML. 1999. High rates of extinction and threat in poorly studied taxa. *Conserv. Biol.* 13:1273–81
65. Master LL, Stein BA, Kutner LS, Hammerson GA. 2000. Vanishing assets. Conservation status of the US species. In *Precious Heritage, The Status of Biodiversity in the United States*, ed. BA Stein, LS Kutner, JS Adams, pp. 93–118. New York: Oxford Univ. Press

66. Pitman NCA, Jørgensen PM. 2002. Estimating the size of the world's threatened flora. *Science* 298:989
67. Pimm SL, Raven P. 2000. Extinction by numbers. *Nature* 403:843–45
68. Ehrlich P, Kremen C. 2001. Human effects on ecosystems, overview. See Ref. 26, 3:383–93
69. Dirzo R, Miranda A. 1991. Altered patterns of herbivory and diversity: a case study of the possible consequences of contemporary defaunation. In *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*, ed. PW Price, TM Lewinsohn, GW Fernandes, WW Benson. New York: Wiley
70. Laurance WF, Bierregaard RO Jr, eds. 1997. *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*. Chicago: Chicago Univ. Press
71. Redford KH. 1992. The empty forest. *BioScience* 42:412–26
72. Brooks TM, Mittermeier RA, Mittermeier CG, Fonseca GAB, DA Rylands AB, et al. 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* 16:909–23
73. Pimm SL, Askins RA. 1995. Forest losses predict bird extinctions in eastern North America. *Proc. Natl. Acad. Sci. USA* 92:9343–47
74. Brooks TM, Pimm SL, Collar NJ. 1997. Deforestation predicts the number of threatened birds in insular Southeast Asia. *Conserv. Biol.* 11:382–94
75. Brooks TM, Balmford A. 1996. Atlantic forest extinctions. *Nature* 380:115
76. Brooks TM, Pimm SL, Oyugi JO. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. *Conserv. Biol.* 15:1140–50
77. Ceballos G, Ehrlich PR. 2002. Mammal population losses and the extinction crisis. *Science* 296:904–7
78. McNeely JA, Harrison J, Dingwall P. 1994. *Protecting Nature: Regional Reviews of Protected Areas*. Cambridge, UK: IUCN Publ. Serv. Unit

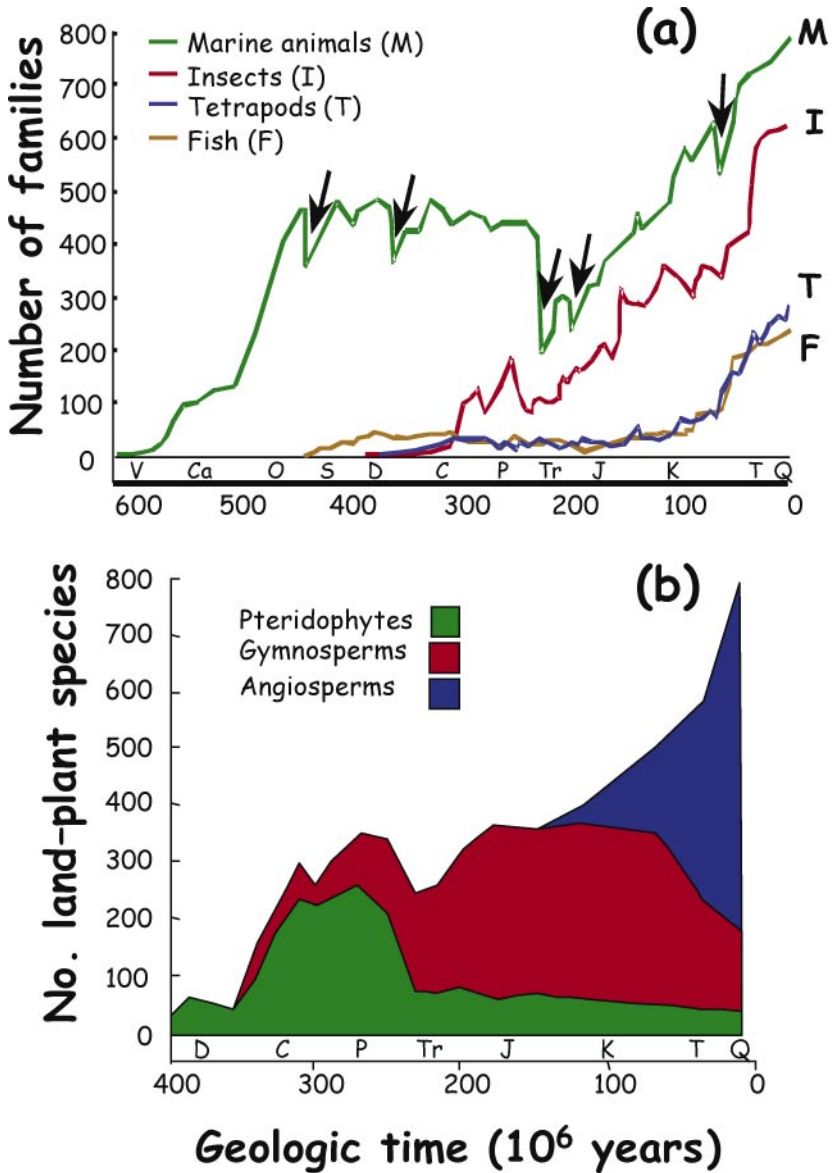
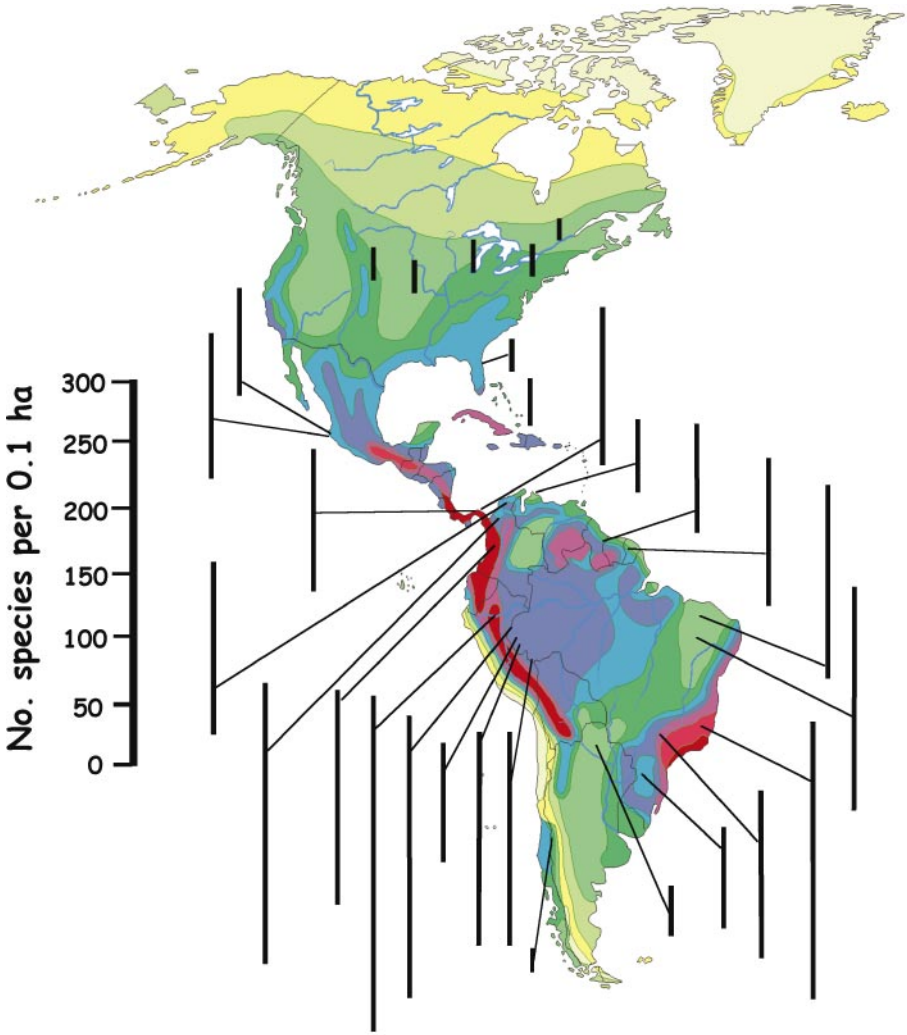












Figure 1 (a) The number of families of marine animals, insects, tetrapods, and fish through the last 600 million years, and (b) the number of land-plant fossil species, including three major groups, Angiosperms, Gymnosperms, and Pteridophytes, through the last 400 million years. The symbols used are: V, Vendian; Ca, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary; and Q, Quaternary. Modified from (11), with permission.



Diversity zones (DZ): number of species per 10,000 km²

 DZ 1 (<100)	 DZ 6 (1500 - 2000)
 DZ 2 (100 - 200)	 DZ 7 (2000 - 3000)
 DZ 3 (200 - 500)	 DZ 8 (3000 - 4000)
 DZ 4 (500 - 1000)	 DZ 9 (4000 - 5000)
 DZ 5 (1000 - 1500)	 DZ 10 (≥ 5000)

See legend on next page

Figure 3 Map of plant species diversity by density surfaces (number of species per 10,000 km²) in the Americas and the number of plant species per 0.1 ha in different localities throughout the region. Each bar represents the average value for lowland sites (up to 1000 m above sea level) located in close proximity within a latitudinal band. (The number of sites for each average value varies. Files with details on site identity and number of species can be obtained from R. Dirzo upon request.) The number of species per 0.1 ha was obtained from data of Alwyn Gentry, reported in (48). The map was modified from (47) in the *Acta Botanica Fennica*, Volume 162, and published with permission of the Finnish Zoological and Botanical Publishing Board and the authors.

CONTENTS

I. EARTH'S LIFE SUPPORT SYSTEMS

- Climate Change, Climate Modes, and Climate Impacts,
Guilin Wang and David Schimel 1
- The Cleansing Capacity of the Atmosphere, *Ronald G. Prinn* 29
- Evaluating Uncertainties in Regional Photochemical Air Quality
Modeling, *James Fine, Laurent Vuilleumier, Steve Reynolds,*
Philip Roth, and Nancy Brown 59
- Transport of Energy, Information, and Material Through the Biosphere,
William A. Reiners and Kenneth L. Driese 107
- Global State of Biodiversity and Loss, *Rodolfo Dirzo and Peter H. Raven* 137
- Patterns and Mechanisms of the Forest Carbon Cycle, *Stith T. Gower* 169

II. HUMAN USE OF ENVIRONMENT AND RESOURCES

- Dynamics of Land-Use and Land-Cover Change in Tropical Regions,
Eric F. Lambin, Helmut J. Geist, and Erika Lepers 205
- Urban Centers: An Assessment of Sustainability, *Gordon McGranahan*
and David Satterthwaite 243
- Water Use, *Peter H. Gleick* 275
- Meeting Cereal Demand While Protecting Natural Resources and
Improving Environmental Quality, *Kenneth G. Cassman,*
Achim Dobermann, Daniel T. Walters, and Haishun Yang 315
- State of the World's Fisheries, *Ray Hilborn, Trevor A. Branch, Billy Ernst,*
Arni Magnusson, Carolina V. Minte-Vera, Mark D. Scheuerell,
and Juan L. Valero 359
- Green Chemistry and Engineering: Drivers, Metrics, and Reduction to
Practice, *Anne E. Marteel, Julian A. Davies, Walter W. Olson,*
and Martin A. Abraham 401

III. MANAGEMENT AND HUMAN DIMENSIONS

- International Environmental Agreements: A Survey of Their Features,
Formation, and Effects, *Ronald B. Mitchell* 429

Tracking Multiple Pathways of Human Exposure to Persistent Multimedia Pollutants: Regional, Continental, and Global Scale Models, <i>Thomas E. McKone and Matthew MacLeod</i>	463
Geographic Information Science and Systems for Environmental Management, <i>Michael F. Goodchild</i>	493
The Role of Carbon Cycle Observations and Knowledge in Carbon Management, <i>Lisa Dilling, Scott C. Doney, Jae Edmonds, Kevin R. Gurney, Robert Harriss, David Schimel, Britton Stephens, and Gerald Stokes</i>	521
Characterizing and Measuring Sustainable Development, <i>Thomas M. Parris and Robert W. Kates</i>	559
Just Oil? The Distribution of Environmental and Social Impacts of Oil Production and Consumption, <i>Dara O'Rourke and Sarah Connolly</i>	587

INDEXES

Subject Index	619
Cumulative Index of Contributing Authors, Volumes 19–28	649
Cumulative Index of Chapter Titles, Volumes 19–28	653

ERRATA

An online log of corrections to *Annual Review of Environment and Resources* chapters may be found at <http://environ.annualreviews.org>