

# **The Winners of the Blue Planet Prize**

**2001**

2001

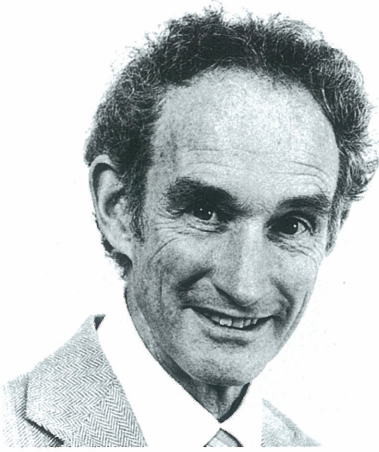
## Blue Planet Prize

**Lord (Robert) May of Oxford  
(Australia)**

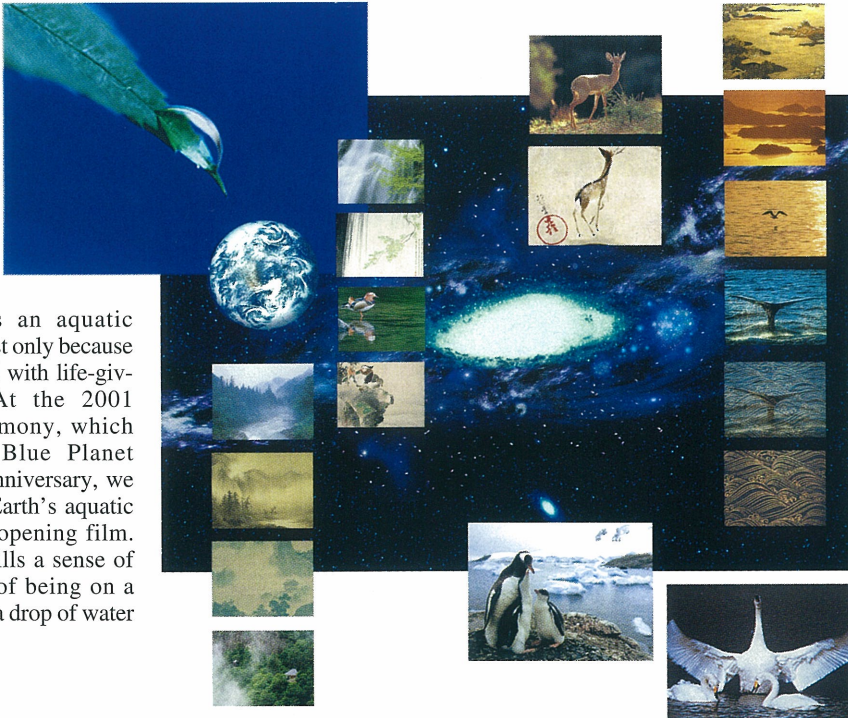
President of the Royal Society of London

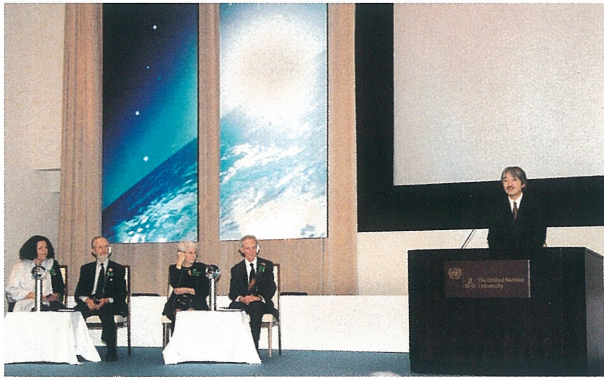
**Dr. Norman Myers  
(U.K.)**

Honorary Visiting Fellow, Green College,  
Oxford University



The Earth is an aquatic planet. We exist only because we are blessed with life-giving water. At the 2001 Awards Ceremony, which marked the Blue Planet Prize's 10th anniversary, we explored the Earth's aquatic nature in the opening film. This film instills a sense of appreciation of being on a planet that is "a drop of water in the galaxy."



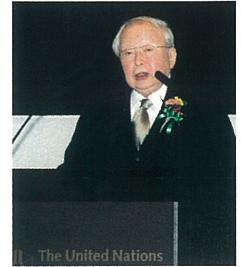


His Imperial Highness Prince Akishino congratulates the laureates.



His Imperial Highness Prince Akishino at the ceremony.

Dr. Jiro Kondo, chairman of the Selection Committee, describes the Blue Planet Prize selection process.



The prizewinners receive their trophies and certificates of merit from Foundation Chairman Hiromichi Seya.



Lord (Robert) May of Oxford



Dr. Norman Myers



The Blue Planet Prize Commemorative Lectures.



John McCarthy, Ambassador of Australia to Japan (left), and Stephen Gomersall, Ambassador of the United Kingdom to Japan (right), congratulate the laureates.

## Profile

# Lord (Robert) May of Oxford

President of the Royal Society of London

### Education and Academic and Professional Activities

- 1936 Born in January in Australia.
- 1956 B. Sc., University of Sydney.
- 1959 Ph.D., Theoretical Physics, University of Sydney.
- 1959-1961 Researcher, Harvard University, U.S.A.
- 1962-1972 Professor, Physics, University of Sydney.
- 1973-1988 Professor, Biology, Princeton University.
- 1979 Fellow, Royal Society of London.
- 1980 Weldon Memorial Prize, Oxford University.
- 1984 MacArthur Award.
- 1988-1995 Professor, Imperial College and Oxford University, United Kingdom.
- 1991 Linnean Medal, Linnean Society.
- 1991 Overseas Member, Australian Academy of Sciences.
- 1992 Inaugural Christian Marsh Prize.
- 1992 Foreign Member, U.S. National Academy of Science.
- 1995 Frink Medal, Zoological Society.
- 1995-2000 Chief Scientific Advisor, Government of the United Kingdom.
- 1996 Crafoord Prize in Biosciences, Royal Swedish Academy of Sciences.
- 1998 Balzan Prize awarded by the President of Italy.
- 2000— President, Royal Society of London.

After pursuing research in theoretical physics at the University of Sydney, Lord (Robert) May of Oxford shifted his focus to mathematical biology. He achieved a solid record of noteworthy accomplishments at Princeton University in the United States before coming to his present post at Oxford University, where he is active as an influential, world-leading academic.

Applying mathematical concepts to biology, he studied the stability of animal populations in 1973, and discovered for the first time that when you increase the number of species, even in complex animal societies, or add more interactions between species, the probability of the system becoming less stable was greater. Furthermore, he uncovered the fact that uni-dimensional nonlinear differential equations often exhibit dynamic states similar to those of animal populations, and founded the new field of “chaotic dynamics” in biology.

Lord May drew attention to the fact that if we wish to manage ecosystems—for example, if we wish to estimate the impact of human fishing on fishing grounds—that we must pay attention to the characteristic changes in the populations. He also investigated how AIDS,

which was transmitted to a different species as a result of environmental change, spreads, utilizing a combination of simplified analytical models and computer simulations to provide the data required to formulate preventative strategies.

In 1995, Lord May was appointed Chief Scientific Advisor to the British Government and Head of the Office of Science and Technology, and was honored in 2000 with election as President of the Royal Society of London. From these elite positions, he continues to counsel for ecological preservation and action to curb various urgent environmental problems.

# Biological Diversity in a Crowded World: Past, Present, and Likely Future

Lord (Robert) May of Oxford

February 2002

How much do we know about the diversity of organisms on our planet? First, estimates of the number of distinct species of plants, animals and fungi (eukaryotes) that have been named and recorded—a simple, factual question, like how many books in the library catalogue—range from 1.4 million to 1.8 million. Second, estimates of the total number of species present on Earth today range over more than an order-of-magnitude, from a low of around 3 million, to a high of 30 million or possibly much more. And third, we have even less idea of the rates at which species may currently be going extinct as a result of habitat destruction, introduced aliens, overexploitation and other consequences of human population growth.

## Numbers of Species Today

The systematic naming and recording of species began relatively recently with Linneaus' canonical work, which in 1758 recognised some 9,000 species. Today, the total number of living species named and recorded is around 1.7 to 1.8 million. Amazingly, no centralised catalogue exists. Around one million of these are insects, of which an estimated 400,000 are beetles. And of these beetles, an estimated 40% are known from only one collecting site, and sometimes from only one specimen. So it is not surprising that there is a problem with synonymy (the same species unwittingly recorded under different names by different researchers). Known rates of synonymy run, on average, around 20%. Recent mathematical studies, however, suggest that if these rates are the ones we know, the true rates are likely to be higher (Solow *et al.*, 1995). My estimate is that we may have named and recorded around 1.5 million species (May, 2000), but this number could be 10% higher or lower. To this total, we are adding around 13,000 new species each year. But at the same time, we are resolving synonymies, so that the net addition is around 10,000 new species each year (Hammond, 1995).

Some groups are much better known than others, reflecting patterns in the taxonomic workforce, which derive from intellectual fashions rather than analytic assessments of priorities. Bird and mammal species are comparatively well documented; even though three to five new bird species and around 10 new mammal species are found each year, such numbers are small fractions of the totals recorded in these classes (approximately 10,000 species of birds and 4,000 of mammals). The roughly 270,000 recorded species of vascular plants probably represent 90% or so of the true total. But comprehensive explorations of invertebrate groups

in previously-unstudied places—tropical canopy insects; deep-sea benthic macrofauna; fungi—typically find 20% to 50%, or even more, of the species are new to science. Taxonomists are distributed roughly evenly between vertebrates, plants and invertebrates. But there are roughly 10 plant species for each vertebrate animal species, and conservative estimates suggest around 100 insect species for each vertebrate one. Thus, current patterns of knowledge reflect the fact that the average vertebrate species receives 10 times more taxonomic effort than the average plant species, and 100 times more than the average invertebrate (Gaston and May, 1992). This is a bad way to run a business.

The true total number of living species is very uncertain. My guesstimate is in the range 5 to 15 million with a favoured figure of perhaps 7 million (May, 2000). Dramatically higher numbers have been proposed: 30-million insects on the basis of studies of beetles in tropical canopies; tens of millions of benthic invertebrates on the basis of a deep-shelf transect off the northeastern U.S.A.; 1.5-million fungi on the basis of scaling up the species ratio of fungi to vascular plants in Britain; and others. I am sceptical of all these estimates, but a true total anywhere in the range 3 to 100 million could turn out to be correct. The fact that reasonable estimates vary so widely says a lot about how little we know.

### **Understanding Diversity**

The lack of systematic compilations of information about recorded species, much less about the true species totals, greatly impedes our understanding of the causes of biological diversity and of the likely consequences of its impending reduction.

Various patterns—some more general than others—have been tentatively documented. None are fully understood (May, 1990, 1999; Wilson, 1992; Lawton, 1995).

- (1) For most groups of organisms, there is a marked “latitudinal species diversity gradient.” This is particularly notable for tree species, where the enormous diversity of tropical forests gives way to the almost monospecific conifer forests of northerly latitudes.
- (2) Other things being equal, there is a relation between a region’s area and the number of species found in it. A tenfold reduction in area (as when a reserve is established and its surroundings modified) roughly halves the number of species; more generally,  $S=cA^z$ , where the constant  $c$  varies from group to group, and the exponent  $z$  is usually in the range 0.2 to 0.3.
- (3) There are broad trends in the relative abundances of species within a community or ecosystem. In old-established communities, these patterns of species relative abundance tend to be more even (often described by a subset of lognormal distributions) than those for early successional or highly disturbed situations. These “canonical” lognormal patterns can be interpreted as arising from the multiplicative interplay of many ecological and evolutionary factors, and the observed species-area relations can be derived from them (under the additional assumption that total numbers of

individuals scale roughly linearly with area).

- (4) The numbers of species in different categories of physical size vary systematically. For terrestrial animals, a decrease by a factor 10 in characteristic linear dimensions (or equivalently, a factor 1,000 in mass) roughly results in 100 times more species. This rough rule holds down to size categories around a few millimetres; species numbers fall away below this. What are the ecological or evolutionary origins of this rough rule, which holds true over four or more orders-of-magnitude in characteristic lengths of animals on land and roughly similarly in the sea (Fenchel, 1993). To what extent—and why—is the breakdown in this rule at small sizes real, and to what extent may it be a consequence of less knowledge about smaller things?
- (5) Patterns in the relations between the body sizes and the geographical ranges of species are only just beginning to receive systematic attention. It is possible that geographical ranges are typically more extensive for relatively large organisms and for microorganisms (protozoa and below) than for mid-size organisms (insects). If true, such patterns, which are entwined with the species-size effects of (4), are relevant, amongst other things, to possible range modifications associated with climate change.

### **Extinction Rates**

The history of life on Earth, written in the fossil record over the past 600-million years since the Cambrian explosion in the diversity of multicellular organisms, is one of broadly increasing diversity, albeit with many fluctuations and punctuated by episodes of mass extinction. As reviewed in more detail elsewhere (Sepkoski, 1992; May, 2000), the average lifespan of a species in the fossil record, from origination to extinction, is typically a few million years (that is, of the order  $10^6$  to  $10^7$  years). There is, however, much variation both within and among groups, and some groups have lifespans significantly longer or shorter than this. Comparing this few-million-year average lifespan with the 600-million-year fossil record span, we might estimate that 1% to 2% of all species ever to have lived are with us today. But, allowing for the fluctuating but steady—very roughly linear—average growth in species diversity since the Cambrian, a better estimate might be 2% to 4%. And if we recognise that most of today's species are terrestrial invertebrates (mainly insects), whose patterns of diversification began around 450-million years ago and whose average lifespan may be characteristically longer than 10-million years, it could be that today's species represent more like 5%, or conceivably even 10%, of those ever to have graced our planet.

Over the past century, rigorously documented extinctions in well-studied groups—primarily birds and mammals—have run around one species per year. Because tropical species typically receive less attention, true extinction rates of birds and mammals are undoubtedly higher. But even one per year among the roughly 14,000 species of birds and mammals translates to expected species' lifetimes, based on documented recent extinction rates, of around  $10^4$  years. Although seemingly long, this is shorter by a factor of order  $10^{-2}$  to  $10^{-3}$  than the back-



ground average lifespan of  $10^6$  to  $10^7$  years seen in the fossil record. That is, recent extinction rates in well-documented groups have run one-hundred to one-thousand times faster than the average background rates.

Looking toward the immediate future, four different approaches to estimating impending rates of extinction suggest species' life expectancies of around a few hundred to one-thousand years. One of these approaches is based on the above-mentioned species-area relations, coupled with assessments of current rates of tropical deforestation or other habitat loss (if tropical forests are being lost at the rate of 1% to 2% each year, the species-area relation implies this commits 0.25% to 0.5% of their species to extinction, which inverts to a rough estimate of species' lifetimes of roughly 200-400 years). Two other methods are based in different ways on the International Union for the Conservation of Nature's (IUCN) current catalogue of "endangered" or "vulnerable" species. As reviewed elsewhere (May *et al*, 1995), one of these estimates the average rate at which species in better-studied groups (birds, mammals and palm trees) are climbing the ladder of IUCN categories of endangerment. This suggests expected species' lifetimes in the range 100 to 800 years in these groups. A more precise variant of this approach uses species-by-species assessments of extinction probability distributions as functions of time. Using 10 vertebrate groups (3, 4, 3 orders or families of reptiles, birds and mammals, respectively), Mace (1994) estimates average species' lifetimes in the range 100 to 1,000 years, and mainly in the 300- to 400-year range for mammals and birds. The fourth method uses models for branching processes in phylogenetic trees, along with recent data for bird and mammal orders, to project average times to extinction within bird and mammal orders (McKinney, 1998). Under a range of assumptions about branching processes, these models suggest species' lifetimes again of the order of a few hundred years (characteristically shorter for mammals than birds). Thus, all four of these methods, each of which is unreliable in its own distinctive way, agree in suggesting a further shortening of expected species' lifetimes to around  $10^2$  to  $10^3$  years.

Such figures correspond to likely extinction rates of a factor of ten thousand, give or take at most an order of magnitude, above background over the next century or so. This represents a sixth great wave of extinction, fully comparable with the Big Five mass extinctions of the geological past, but different in that it results from the activities of a single other species rather than from external environmental changes.

As we face this future, we must ask: does it matter more if we lose 25% of all mammal species than if we lose 25% of the vastly more numerous insect species? Or does it matter equally? Or less? There is need not only for more taxonomic information, but also for a "calculus of biodiversity" based on this information. Such a calculus should, ideally, quantify the taxonomic uniqueness, or amount of independent evolutionary history, inherent in individual species (Vane-Wright *et al*, 1991; Nee and May, 1997). I would like to see such quantification, along with more explicit recognition of constraining political, economic and social realities, replace emotion in assigning conservation priorities and places on the Ark (although emotional elements should, certainly, also be part of such a quantification). For further review and remarks on this topic, see May *et al* (1995).

## Why Value Biological Diversity?

One argument for the preservation of biological diversity is narrowly utilitarian. It correctly emphasises the benefits already derived from natural products, such as foods, medicines and so on. Currently, 25% of the drugs on the shelves in the pharmacy derive from a mere 120 species of plants. But, throughout the world, the traditional medicines of native peoples make use of around 25,000 species of plants (about 10% of the total number of plant species). We have much to learn. More generally, as our understanding of the natural world advances, both at the level of new species and at the level of the molecular machinery from which all organisms are self-assembled, the planet's genetic diversity is increasingly the raw stuff from which our future can be constructed. It seems a pity to be burning the books before we can read them, and before we can create wealth from the recipes on their pages.

Another class of arguments is more diffusely utilitarian. The interactions between biological and physical processes created and maintain the earth's biosphere as a place where life can flourish. With impending changes in climate caused by the increasing scale of human activity, we should be worried about reductions in biological diversity, at least until we understand its role in maintaining the planet's life support systems. The first rule of intelligent tinkering is to keep all the pieces.

For me, however, a third class of argument is the most compelling. It is clearly set out by the U.K. Government in *This Common Inheritance* (HMSO, 1990, ch 1.14). It is "the ethical imperative of stewardship ... we have a moral duty to look after our planet and hand it on in good order to future generations." This argument is, however, easier to sustain for those privileged to live in affluent developed countries. Were I struggling to feed my fifth child in abject poverty in some areas of the developing world, I suspect I would find this ethical argument less compelling.

## Conclusion

The previous century has seen more advances in our understanding of the natural world than has all previous human history. We have applied this scientific understanding to improve lives in both developed and developing countries. We are, however, now beginning to realise some of the unintended adverse consequences of well-intentioned actions. Arguably the most significant is accelerating loss of biological diversity. What happens to our world, and to us and the creatures we share the world with, in the future depends on the actions we take now. As a new century dawns, our greatest challenge remains to ensure that necessary increases in global productivity are achieved in a sustainable and environmentally friendly way.

I believe these are matters of concern for all of us. But effective action must be based on good scientific understanding of the underlying causes, and likely consequences, of loss of biological diversity.

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## Lecture

# Biological Diversity: Causes, Consequences, and Conservation

Lord (Robert) May of Oxford

### Introduction

I am honoured to receive the 2001 Blue Planet Prize. Also I am very aware that I receive this prize as a symbolic representative of the large community of scientists, who in recent years have greatly advanced our understanding of the causes and consequences of biological diversity, and of growing threats to it. I especially commend the Asahi Glass Foundation for establishing this Prize in recognition of the importance of environmental and conservation science.

Properly to understand how today's rich and varied plant and animal life came to be here, we need to answer underlying ecological questions. How does the structure of the web of interactions among species affect communities' ability to recover from disturbance or to resist invasion? What factors determine the observed variety of patterns of species abundance, of commonness and rarity? More generally, what determines species numbers in different places? Above all, what are the various causes of observed extinctions, and to what extent are extinction rates currently accelerating? In what follows, I will sketch answers to some of these questions, and also will indicate remaining areas of uncertainty.

### Structure of Ecosystems

**Earlier Ideas.** Around 1970, the conventional wisdom—set out in textbooks, following the work of the pioneering ecologists, Charles Elton and Evelyn Hutchinson—was that “complex” communities (those with more species and/or richer webs of connections among them) were more “stable” (better able to resist or recover from disturbance, human-created or natural). Comparing mathematical models for ecological communities with few species against the corresponding models with many species, I showed there could be no such simple and general rule; all things being equal, complex systems are likely to be more dynamically fragile. This and other related work was drawn together in the monograph *Stability and Complexity in Model Ecosystems* (1973, with a second edition in 1974). In 2001, Princeton University Press reissued this book, with introductory “retrospective thoughts,” in its *Landmarks in Biology* series.

**Ecosystem Stability and Complexity.** I believe this work helped to refocus the agenda for studies of the structure and function of ecosystems. For one thing, we have become more careful about distinguishing the productivity of a community of interacting plants and animals, as a whole, from the productivity and fluctuations in the individual populations that constitute the community. Recent studies by Tilman *et al* (1996, 1998), Naeem and Li (1997) and others

tend to bear out my earlier suggestions that increasing complexity or diversity, in the sense of a larger number of constituent species in the community (larger “species richness”), tends to make for greater stability in total productivity, but that individual species are liable to greater fluctuations in abundance in such communities. For another thing, it has become clear that increasing numbers of interactions among species in a foodweb (increasing “connectance”) does not automatically enhance ability to resist disturbance; instead, current efforts seek to understand the special kinds of interconnectedness among subsets of species that reconcile complexity with stability in particular ecosystems (McCann *et al.*, 1998).

**A Contemporary Synthesis?** More broadly, my own view is that, over evolutionary time, ecosystems are in tension between two opposing forces. On the one hand, evolution tends to favour every opportunity, every niche, being exploited, making for increasing diversity over time. On the other hand, more species-rich communities in general are more dynamically fragile, tending to set limits to diversification. In relatively environmentally predictable settings, such as tropical rainforests or some coral reefs, the trade-off between these two countervailing pressures is set at a point corresponding to more species-rich communities. In harsher and less predictable environments, such as boreal forests or estuaries, the trade-off results in relatively simpler communities. In both cases, the set point is determined by the acceptable average degree of fluctuation in individual populations, which is broadly similar—over the long run—in all cases. As noted above, this cuts across the earlier conventional wisdom, but seems increasingly in accord with observations about levels of fluctuation in tropical communities, and in various field experiments.

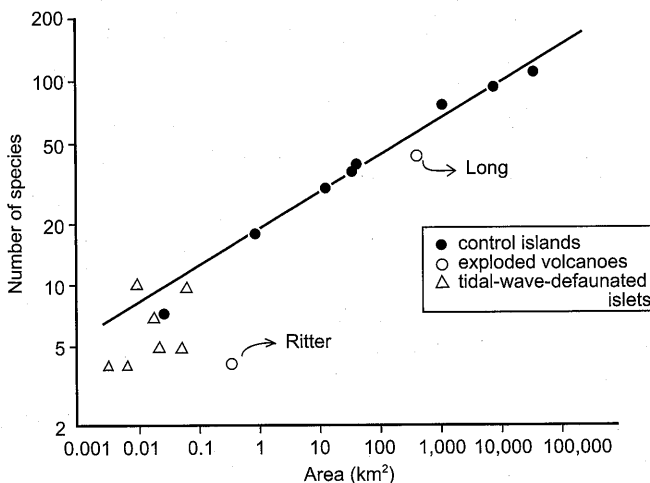
### **Patterns in the Distribution and Abundance of Species**

**Species Relative Abundance.** There are broad trends in the relative abundances of species within a community or ecosystem. In old-established communities, these patterns of species relative abundance tend to be more even (often described by a subset of lognormal distributions) than those for early successional or highly disturbed situations. Such “canonical” lognormal patterns can be interpreted as arising from the multiplicative interplay of many ecological and evolutionary factors. These patterns have implications, amongst other things, for understanding the different kinds of “rarity” (Rabinowitz *et al.*, 1986; Gaston, 1994); see Table 1. In particular, they imply that to be rare is by no means necessarily to be in danger of extinction. This latter point appears frequently to be misunderstood: for example, the current IUCN Red List of Threatened Plants (Walter and Gillett, 1997) unaccountably, and unlike the corresponding animal lists, treats all “rare” plants as threatened.

**Table 1.** The distribution of 160 plant species from the *Biological Flora of the British Isles*, classified into eight categories according to geographic distribution (wide or narrow), habitat specificity (broad or restricted), and local abundance (somewhere large or everywhere small). We would recognise the circled category (wide distribution, broad range of habitats, locally abundant somewhere) as “common;” the other seven categories represent “seven kinds of rarity” (after Rabinowitz *et al*, 1986).

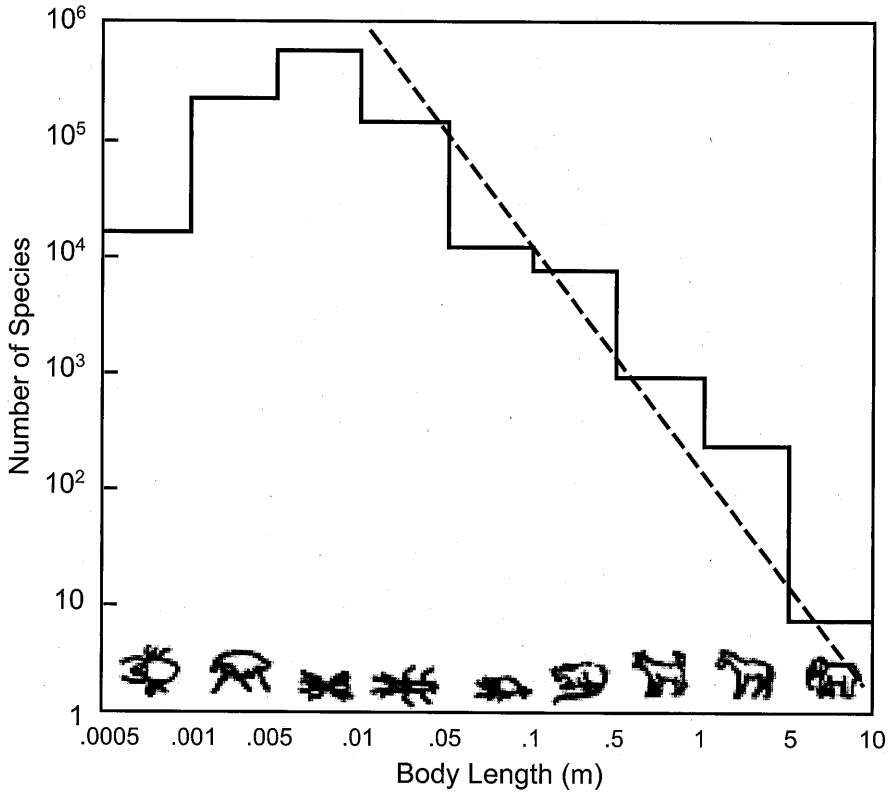
Local population size	Geographic distribution			
	Wide habitat specificity		Narrow habitat specificity	
	Broad	Restricted	Broad	Restricted
Somewhere large	(58)	71	6	14
Everywhere small	2	6	0	3

**Species-Area Relations.** Other things being equal, there is a relation between a region’s area and the number of species found in it. A tenfold reduction in area (as when a reserve is established, and its surroundings modified) roughly halves the number of species. More generally, there is a power law relationship,  $S = cA^z$ ; here  $S$  denotes the number of species,  $A$  the area,  $c$  is a constant which varies from group to group, and the exponent  $z$  is usually in the range 0.2-0.3. Figure 1 gives an illustrative example. Interestingly, this relation follows from the “canonical” lognormal distribution of species relative abundance mentioned above, combined with the additional assumption that total numbers of individuals scale roughly linearly with area (for a recent review, see May and Stumpf, 2000). Given the shakiness of these theoretical assumptions, it is perhaps surprising that the species-area relationship is so widely found in nature. It has important implications. In particular, we shall see below how it can be used to make tentative projections about future extinction rates.



**Figure 1.** An example of the relation between species number and island area in an archipelago: number of resident, nonmarine, lowland bird species  $S$  on islands in the Bismarck Archipelago, plotted as a function of island area on a double logarithmic scale. The solid circles represent relatively undisturbed islands, and the straight line  $S = 18.9A^{0.18}$  was fitted by least-mean-squares through the points for the seven largest islands. The open circles refer to the exploded volcanoes, Long and Ritter, where species number is still below equilibrium, especially on Ritter, because of incomplete regeneration of vegetation. The open triangles refer to coral islets inundated by the Ritter tidal wave in 1888. (From Diamond, 1974).

**Numbers of Species in Relation to their Physical Sizes.** The numbers of species of animals in different categories of physical size vary systematically. For terrestrial animals, a decrease by a factor 10 in characteristic linear dimensions (or, equivalently, a factor 1,000 in mass) roughly results in 100 times more species (May, 1978); see Figure 2. This rough rule holds down to size categories around a few millimetres; species numbers fall away below this. What are the ecological or evolutionary origins of this rough rule, which holds true over four or more orders-of-magnitude in characteristic lengths of animals on land, and roughly similarly in the sea (Fenchel, 1993)? To what extent—and why—is the breakdown in this rule at small sizes real, and to what extent may it be a consequence of less knowledge about smaller things?



**Figure 2.** A crude estimate of the distribution of all terrestrial animals categorized according to characteristic length  $L$ . The dashed line indicates the relation  $S \sim L^{-2}$ , as in Fig. 3 ( $S$  = number of species). (After May, 1978)

**Body Sizes and Geographical Ranges.** Patterns in the relations between the body sizes and the geographical ranges of species are only just beginning to receive systematic attention. It is possible that geographical ranges are typically more extensive for relatively large organisms and for microorganisms (protozoa and below) than for mid-size organisms (insects). If true, such patterns—which are entwined with the species-size effects mentioned immediately above—are relevant, amongst other things, to possible range modifications associated with climate change.

**Patterns in Foodweb Structure.** It has been strongly argued that each plant or animal species in a foodweb typically is connected—eating or being eaten—with only 3 to 5 other species. Why so roughly constant a number, and why so small? Also, the lengths of food chains in such webs—the number of links connecting the primary producing plants, through the animals eating them, and those eating them, and so on, to the top predators—typically are only 3 to 4 links long, with surprisingly little variation within and among foodwebs. Again, why so roughly constant a rule, and why are chains so short? Although these important empirical patterns (Pimm et al, 1991) may in part be artifacts of the way humans gather and analyse complicated data, there are important questions here. Various explanations currently contend: efficiency of energy transfer from level to level within a foodchain; relations between the dynamics of the system and its structure; evolutionary instability of excessively complex chains; and others. But every explanation proposed so far has important weaknesses.

**Connections Among Seemingly Different Questions.** To illustrate how the above questions are intimately entwined with seemingly simpler questions of how many species there are on earth, consider the relation between foodweb patterns and global species numbers. If we really had a fundamental understanding of how foodweb structure was determined by evolutionary and ecological factors in specific environments, we could predict the average ratio between the number of animal species and the number of primary producing plant species that ultimately sustain them, in foodwebs in particular environments, and thence the overall global average such ratio. We can be fairly certain, to within 10% or so, that the global total of plant species is around 300,000. So if we knew the animal/plant species ratio, we could assess the total number of animal species, by this indirect argument based on understanding ecosystem structure. Unfortunately, we have no such understanding. Such rough empirical data as are available suggest that the animal/plant species ratio is around 10 in foodwebs, although with much variation from place to place. This very rough empirical estimate suggests a global total of about 3-million animal species; we shall return to this below.

### **Dynamics of Plant and Animal Populations**

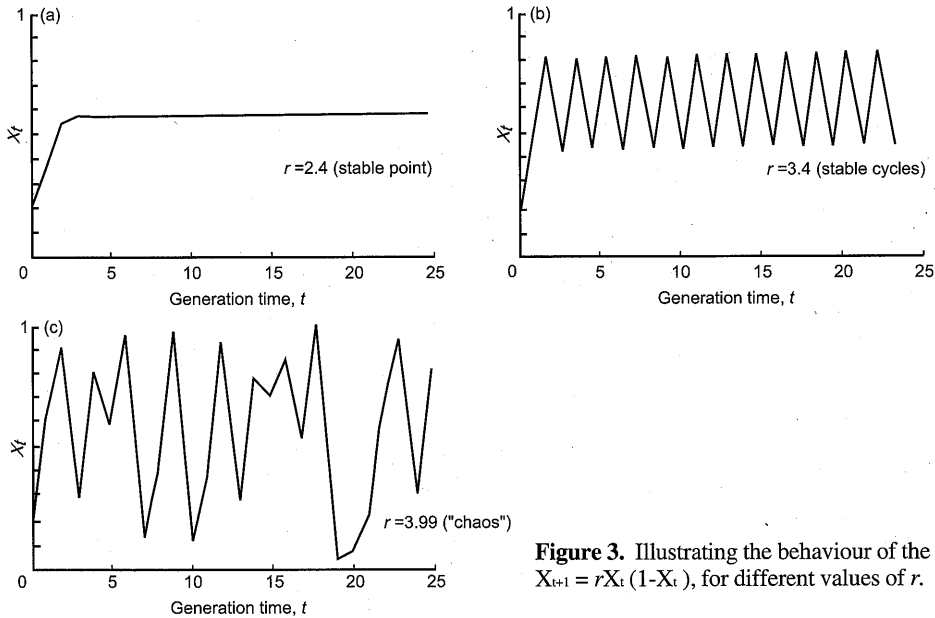
Another, very different, strand of my work is ultimately related to biodiversity, because of the surprising light it sheds on how populations can react to disturbance.

**The Balance of Nature?** Early work on “the balance of nature” implicitly tended to assume that population numbers would be roughly steady, unchanging from year to year, unless affected by environmental fluctuations. But the factors regulating the densities of plant and animal populations—food supplies, predators, infectious diseases, nest sites or other territorial considerations, and many others—tend to operate in a nonlinear way. That is, the strengths of the feedbacks that govern the possible steady or “equilibrium” population size themselves depend on population size, so that if the population doubles, it does not simply mean that per capita birth rates and death rates double; birth rates may fall, and death rates rise, more than proportionately or “linearly.” This is what “nonlinear” means. In effect, two plus two does not necessarily add up to four when the governing mechanisms are nonlinear.

**Chaos and Other Surprises.** The simplest nonlinear equations representing how biological populations may be regulated by feedback mechanisms can exhibit a bewildering,



almost magical, array of behaviour. The simplest such equations, of the kind suggested by various people working on insect and on fish populations as descriptions of their systems, can—although purely deterministic, with no statistical elements—give rise not only to the expected constant “equilibrium” solutions, but alternatively to stable and self-generated cycles of boom and bust, or even more surprisingly, to apparently random fluctuations. For a population, such as many temperate insects, with discrete non-overlapping generations (adults appearing each year, laying eggs to develop into next year’s adults, then dying), a simple metaphor is  $X_{t+1} = rX_t(1 - X_t)$ . Here  $X_t$  is the population in year  $t$ , scaled so that if  $X$  ever gets as large as 1, it extinguishes itself, and  $r$  is its intrinsic growth rate at low density (when  $X$  is close to 0). As can be verified by iterating this simple equation on a hand-held calculator, if  $r$  is between 1 and 3, this equation describes a population that settles to a constant equilibrium value, as earlier ecological intuition required. If  $r$  is above 3 but below about 3.57, we see self-sustained cycles. For  $r$  bigger than 3.57, but below 4, there is “chaos,” apparently random fluctuations, generated by this trivially simple deterministic equation. This behaviour is illustrated in Figure 3.



**Figure 3.** Illustrating the behaviour of the equation  $X_{t+1} = rX_t(1 - X_t)$ , for different values of  $r$ .

**General Implications of Chaos.** This observation, motivated by purely ecological questions, was one of the strands that brought chaos centre stage across the sciences (May, 1974, 1976; the other strand was Lorenz’s (1963) meteorological metaphor, based on a more complicated set of three differential equations). The recognition that simple and fully deterministic rules or equations can generate dynamical patterns that are effectively indistinguishable from random noise has very deep implications for science. It effectively marks the end of

the Newtonian dream that knowing the rules will enable prediction; predicting local weather beyond about 10–15 days is not just a problem of computational power, but of the inherent unpredictability of chaotic dynamical systems.

**Ecological Implications of Chaos.** The implications of cyclic and, even more, of chaotic, dynamics for ecology are widespread. Often the “balance of nature” is disturbed by environmental fluctuations; this has long been recognised. But often the “balance of nature” is inherently cyclic or irregularly fluctuating, driven by the nonlinear dynamics of its own regulatory mechanisms. We have yet fully to realise the implications of this work for understanding the causes and consequences of biological diversity (May, 1985).

## **Biodiversity**

**What is the State of our Knowledge?** Against the background of ecological questions sketched above, how well do we know the world of plants, animals and microorganisms with which we share this planet? The answer, by any one of a variety of objective measures, must be: not very well. First, estimates of the number of species that have been named and recorded (a simple factual question, like how many books in the library catalogue) range from 1.4 million to 1.8 million. Second, estimates of the total number of species present on Earth today range over more than an order-of-magnitude, from a low of around 3 million to a high of 30 million or possibly much more. And third, we have even less idea of the rates at which species may currently be going extinct, as result of habitat destruction and other consequences of human population growth.

**Some Personal Estimates.** In this brief overview, I outline my own best guess of the answers to these three questions. For the number of distinct species named and recorded, I emphasise the uncertainties caused by unresolved synonymies. For the likely total number of living species, I set out my reasons for leaning to the lower end of the range of published estimates. And for present and likely future extinctions, I sketch a relatively precise approach, based on comparative rates of extinction, which avoids some of the imprecisions inherent in dealing with total number of species.

**Numbers of Named Species: Background.** The systematic naming and recording of species began relatively recently, with Linneaus’ standard work, which in 1758 recognised some 9,000 species. Today the total number of living species named and recorded has been estimated at around 1.7 to 1.8 million. Amazingly, no centralised catalogue exists. There are synoptic and computerised catalogues for some better-known groups, most notably birds and mammals. But more than half (roughly 56%) of all named species are insects, and the majority of these are still on card catalogues in individual museums and other collections. By one estimate, around 40% of all named beetle species are known from only one site, and many from only one specimen. In short, the amount of taxonomic effort varies very widely from group to group, with roughly one-third of all taxonomists working on vertebrates, another third working on the 10-times more numerous plant species, and the remaining third working on invertebrate animals, which outnumber vertebrate species by at least a factor of 100 (see Table 2).

**Table 2.** The taxonomy of taxonomists: a rough estimate of the distribution of the taxonomic workforce among broad taxonomic groups, in Australia, U.S.A. and U.K. (after Gaston and May 1992).

	Plants	Animals		Microorganisms	Fossils
		Vertebrates	Invertebrates		
Approximate division of workforce (%)	30	25	35	2-3	5
Estimated total number of living species (Thousands)	300	45	3,000 +	?	-

**Numbers of Named Species: Problems.** Hammond's (1995) assessment for the IUCN of the total number of distinct species that have been named and recorded emphasises the uncertainties caused by synonyms. His survey estimates that around 13,000 new species are currently named each year, but current rates of resolving synonymies—the same species inadvertently given different names by different people in different collections—reduce this number to around 10,000 distinct new species added yearly to the known total. In effect, this corresponds to a synonymy rate of around 20% in named species, a figure elsewhere cited as representative on more direct grounds (Solow et al, 1995). Of course, any such assessment of known synonymy rates must be a lower limit, with other synonyms yet to be uncovered or accumulating in new work. Solow et al (1995) have made a start on this important problem, suggesting the true synonymy rate may be more like 40%.

**Numbers of Named Species: A Current Estimate.** Allowing for all this, my recent assessment (May, 1999) is that the current global total of distinct eukaryotic species (broadly, plants, animals and fungi) that have been named and recorded is around 1.5 million. This is lower than Hammond's (1995) 1.74 million, but is consistent with Wilson's (1988) estimate of 1.4 million ten years ago (augmented by 0.01 million each year for 10 years). See Table 3.

**Table 3.** Number of named, distinct species of eukaryotes (in thousands)

Group	Hammond (1995)	May (1999)
Protozoa	40	40
Algae	40	40
Plants	270	270
Fungi	70	70
<u>Animals</u>	<u>1,320</u>	<u>1,080</u>
Vertebrates	45	45
Nematodes	25	15
Molluscs	70	70
Arthropods	1,085	855
(crustaceans)	(40)	(40)
(arachnids)	(75)	(75)
(insects)	(950)	(720)
(other)	(20)	(20)
others	95	95
Total	1,740	1,500

**Total Number of Species Living Today.** The true total of extant species, as distinct from those we have named and recorded, is hugely uncertain. My recent assessment of the evidence and uncertainties led to a guess of around 7 million in total, with a plausible range of 5 to 15 million (May, 1999). This is lower than Hammond's (1995) guess of 12-million eukaryotic species, but higher than other estimates which are as low as 3 million or so species in total. Estimates as low as 3 million, or as high as 100 million or more, can be defended. See Table 4.

**Table 4.** Estimated total numbers of living species (in thousands)

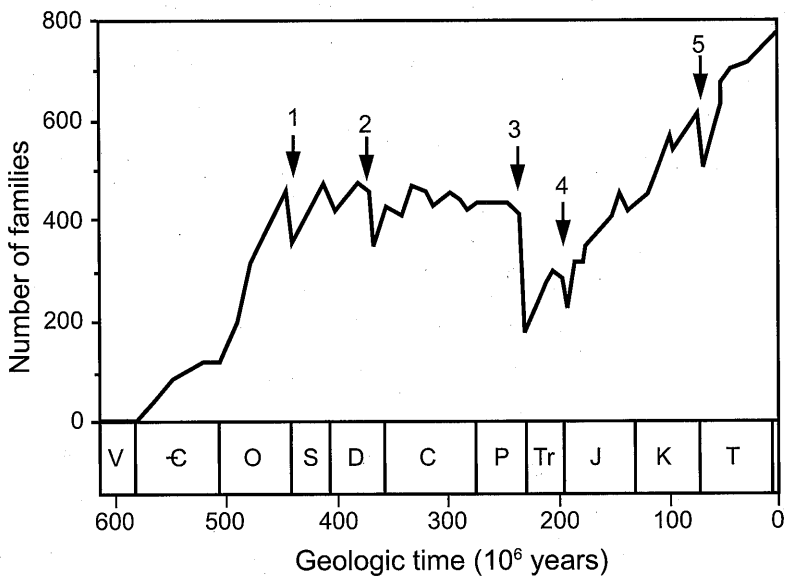
Group	Hammond (1995)		May (1999)
	High – low	Working Figure	
Protozoa	200 – 60	200	100
Algae	1,000 – 150	400	300
Plants	500 – 300	320	320
Fungi	2,700 – 200	1,500	500
Animals	100,000 – 3,000	9,800	5,570
<i>Verts</i>	55 – 50	50	50
<i>Nematodes</i>	1,000 – 100	400	500
<i>Molluscs</i>	200 – 100	200	120
<i>Arthropods</i>	100,000 – 2,400	8,900	4,650
<i>(crust)</i>	(200 – 75)	(150)	(150)
<i>(arachnids)</i>	(1,000 – 300)	(750)	(500)
<i>(insects)</i>	(100,000 – 2,000)	(8,000)	(4,000)
<i>others</i>	800 – 200	250	250
Total	100,000 – 3,500	12,200	6,800
Range	:	100 - 3 million	
Plausible range	:	15 - 5 million	
Best guess	:	7 million	

**Total Number of Species: Further Comments.** All such estimates are dominated by insect totals. I favour an estimate of around 4-million insect species in total, partly based on the methods developed by Gaston and Hudson (1994). This is lower than Hammond's 8-million insects species, but higher than other estimates of around 2 million, either of which could be correct. My total also reflects a distrust of the dramatic upward revision of fungal species numbers by Hawksworth (1991) and of marine macrofaunal species by Grassle and Maciolek (1992), amongst other things. For more detailed reviews of these hugely important issues, see May (1990, 1994, 1999).

## EXTINCTION RATES

**The Past.** The history of life on Earth, written in the fossil record over the past 600-million years since the Cambrian explosion in the diversity of multicellular organisms, is one of broadly increasing diversity, albeit with many fluctuations and punctuated by episodes of mass

extinction; see Figure 4. As reviewed in more detail elsewhere (Sepkoski, 1992; May, 1999), the average lifespan of a species in the fossil record, from origination to extinction, is typically a few million years (that is, of the order  $10^6$  to  $10^7$  years); there is, however, much variation both within and among groups, and some groups have lifespans significantly longer or shorter than this; see Table 5. Comparing this few-million-year average lifespan with the 600-million-year fossil record span, we might estimate that 1%-2% of all species ever to have lived are with us today. But, allowing for the fluctuating but steady—very roughly linear—average growth in species diversity since the Cambrian, a better estimate might be 2%-4%. And if we recognise that most of today's species are terrestrial invertebrates (mainly insects), whose patterns of diversification began around 450-million-year ago and whose average lifespan may be characteristically longer than 10-million-year, it could be that today's species represent more like 5%, or conceivably even 10%, of those ever to have graced our planet.



**Figure 4.** The history of the diversity of marine animal families, as shown by the fossil record over time. The curve connects 77 discrete data points, each giving the total number of well-skeletonized families from a particular stratigraphic stage. The arrows indicate the Big Five episodes of mass extinction. The length of the various geological epochs are indicated on the time axis (V, Vendian; -C, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary).

**Table 5.** Estimated lifespans, from origination to extinction, of various taxa in the fossil record (measured in millions of years). The first part of the Table is after May *et al* (1995), whereas the second part is a new compilation by Robin Cocks (Natural History Museum, London).

TAXON	Date of estimate	Average lifespan (million years)
Part I : References in May <i>et al</i> (1995)		
All invertebrates	Raup (1978)	11*
Marine invertebrates	Valentine (1970)	5 – 10
Marine animals	Raup (1991)	4
Marine animals	Sepkoski (1992)	5*
All fossil groups	Simpson (1952)	0.5 – 5
Mammals	Martin (1993)	1
Cenozoic mammals	Raup and Stanley (1978)	1 – 2
Diatoms	Van Valen (1973)	8
Dinoflagellates	Van Valen (1973)	13
Planktonic foraminifers	Van Valen (1973)	7
Cenozoic bivalves	Raup and Stanley (1978)	10
Echinoderms	Durham (1970)	6
Silurian graptolites	Rickards (1977)	2
		6 – 7
Part II : Information compiled by R. Cocks		
Silurian graptolites	Koren and Rickards (1996)	0.2
Cambrian trilobites	Davidek <i>et al</i> , in press	0.4
Brachiopods	R. Cocks, pers. comm.	0.5
Rodents	R. Cocks, pers. comm.	0.3 – 1.0
Perrissodactyls	R. Cocks, pers. comm.	0.5
Insectivores	J.J. Hooker, pers. comm.	3
Corals (tertiary-recent)	Budd <i>et al</i> , (1996)	0.2 – 7
		(average 4)
Forams	Buzas and Culver (1984)	14 – 16
Coccoliths	J.R. Young, pers. comm.	c. 10

**Recent Extinctions.** Over the past century, rigorously documented extinctions in well-studied groups—primarily birds and mammals—have run around one species per year. Because tropical species typically receive less attention, true extinction rates of birds and mammals are undoubtedly higher. But even one per year among the roughly 13,000 species of birds and mammals translates to expected species' lifetimes, based on documented recent extinction rates, of around  $10^4$  years. Although seemingly long, this is shorter by a factor of order  $10^{-2}$  to  $10^{-3}$  than the background average lifespan of  $10^6$  to  $10^7$  years seen in the fossil record. That is, recent extinction rates in well-documented groups have run one-hundred to one-thousand times faster than the average background rates.

**Guesses About Tomorrow.** Looking toward the immediate future, four different approaches to estimating impending rates of extinction suggests species' life expectancies of around a few hundred to one-thousand years. One of these approaches is based on the above-mentioned species-area relations, coupled with assessments of current rates of tropical deforestation or other habitat loss (if tropical forests are being lost at the rate of 1%-2% each year, the species-area relation implies this commits 0.25%-0.5% of their species to extinction, which inverts to a rough estimate of species' lifetimes of roughly 200-400 years). Two other methods are based in different ways on the International Union for the Conservation of Nature's (IUCN's) current catalogue of "endangered" or "vulnerable" species. As reviewed elsewhere (May *et al.*, 1995), one of these estimates the average rate at which species in better-studied groups (birds, mammals, palm trees) are climbing the ladder of IUCN categories of endangerment; this suggests expected species' lifetimes in the range 100 to 800 years in these groups. A more precise variant of this approach uses species-by-species assessments of extinction probability distributions as functions of time. Using 10 vertebrate groups (3, 4, 3 orders or families of reptiles, birds and mammals, respectively), Mace (1994) estimates average species' lifetimes in the range 100 to 1,000 years, and mainly in the 300- to 400- year range for mammals and birds. The fourth method uses models for branching processes in phylogenetic trees, along with recent data for bird and mammal orders, to project average times to extinction within bird and mammal orders (McKinney, 1998); under a range of assumptions about branching processes, these models suggest species' lifetimes again of the order of a few-hundred years (characteristically shorter for mammals than birds). Thus, all four of these methods, each of which is unreliable in its own distinctive way, agree in suggesting a further shortening of expected species' lifetimes, to around  $10^2$  to  $10^3$  years.

**The Sixth Wave of Extinction.** Such figures correspond to likely extinction rates of a factor of ten thousand, give or take at most an order of magnitude, above background, over the next century or so. This represents a sixth great wave of extinction, fully comparable with the Big Five mass extinctions of the geological past, but different in that it results from the activities of a single other species rather than from external environmental changes.

**A Calculus of Biodiversity?** As we face this future, we must ask: does it matter more if we lose 25% of all mammal species than if we lose 25% of the vastly more numerous insect species? Or does it matter equally? Or less? There is need not only for more taxonomic information, but also for a "calculus of biodiversity" based on this information. Such a calculus should, ideally, quantify the taxonomic uniqueness, or amount of independent evolutionary history, inherent in individual species (Vane-Wright *et al.*, 1991; Nee and May, 1997). I would like to see such quantification, along with more explicit recognition of constraining political, economic and social realities, replace emotion in assigning conservation priorities and places on the Ark (although emotional elements should, certainly, also be part of such a quantification). For further review and remarks on this topic, see May *et al.* (1995).

### **Why Value Biological Diversity?**

**A Narrowly Utilitarian Argument.** One argument for the preservation of biological diversity is narrowly utilitarian. It correctly emphasises the benefits already derived from nat-

ural products, as foods, medicines and so on. Currently, 25% of the drugs on the shelves in the pharmacy derive from a mere 120 species of plants. But, throughout the world, the traditional medicines of native peoples make use of around 25,000 species of plants (about 10% of the total number of plant species); we have much to learn. More generally, as our understanding of the natural world advances, both at the level of new species and at the level of the molecular machinery from which all organisms are self-assembled, the planet's genetic diversity is increasingly the raw stuff from which our future can be constructed. It seems a pity to be burning the books before we can read them, and before we can create wealth from the recipes on their pages.

**A Broadly Utilitarian Argument.** Another class of arguments is more diffusely utilitarian. The interactions between biological and physical processes created and maintain the earth's biosphere as a place where life can flourish. With impending changes in climate caused by the increasing scale of human activity, we should be worried about reductions in biological diversity, at least until we understand its role in maintaining the planet's life support systems. The first rule of intelligent tinkering is to keep all the pieces.

**An Ethical Argument.** For me, however, a third class of argument is the most compelling. It is clearly set out by the U.K. Government in *This Common Inheritance* (HMSO, 1990, ch 1.14): it is "the ethical imperative of stewardship ... we have a moral duty to look after our planet and hand it on in good order to future generations."

## Conclusion

The previous century has seen more advances in our understanding of the natural world than has all previous human history. We have applied this scientific understanding to improve lives in both developed and developing countries. We are, however, now beginning to realise some of the unintended adverse consequences of well-intentioned actions: arguably the most significant is the accelerating loss of biological diversity. What happens to our world, and to us and the creatures we share the world with, in the future depends on the actions we take now. As a new century dawns, our greatest challenge remains to ensure that necessary increases in global productivity are achieved in a sustainable and environmentally friendly way.

I believe these are matters of concern for all of us. But effective action must be based on good scientific understanding of the underlying causes, and likely consequences, of loss of biological diversity.

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