The Winners of the Blue Planet Prize

2001

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Blue Planet Prize

Lord (Robert) May of Oxford (Australia)

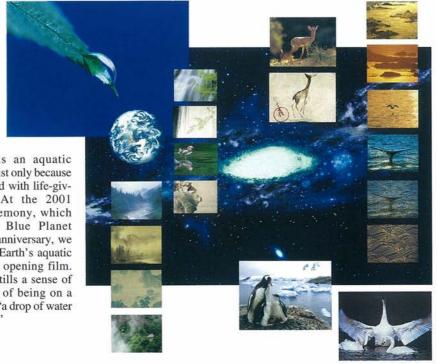
President of the Royal Society of London

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 at the ceremony.

His Imperial Highness Prince Akishino congratulates the laureates.

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 Poyal 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 unidimensional 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.

Essay

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.

Uuderstanding 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 10⁶ to 10⁷ 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 10⁴ years. Although seemingly long, this is shorter by a factor of order 10⁻² to 10⁻³ than the background average lifespan of 10⁶ to 10⁷ 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 10² to 10³ 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.

References

Fenchel, T. "There are More Small than Large Species?" Oikos, 68 (1993), 375–378.
Gaston, K.J. and R.M. May. "The Taxonomy of Taxonomists." Nature, 356 (1992), 281–281.
Hammond, P.M. "The Current Magnitude of Biodiversity." In Global Biodiversity Assessment. Ed. V.H. Heywood. 113–128. Cambridge: Cambridge Univ. Press, 1995.

HMSO. This Common Inheritance: Britain's Environment Strategy. London: HMSO, 1992.

Lawton, J.H. "Population Dynamics Principles." In Extinction Rates. Ed. J.H. Lawton and R.M. May. 147–163. Oxford University Press, 1995.

- McKinney, M.L. "Branching Models Predict Loss of Many Bird and Mammal Orders within Centuries." Anim. Consv., 1 (1998), 159–164.
- Mace, G.M. "An Investigation into Methods for Categorizing the Conservation Status of Species." In Large Scale Ecology and Conservation Biology. Ed. P.J. Edwards, R.M. May and N.R. Webb. 295–314. Oxford: Blackwell, 1994.

May, R.M. "How Many Species?" Phil. Trans. Roy. Soc., B330 (1990), 292-304.

May, R.M. "Unanswered Questions in Ecology." Phil. Trans. Roy. Soc., B354 (1999), 1951-1959.

May, R.M. "The Dimensions of Life on Earth." In *Nature and Human Society: the Quest for a Sustainable World*. Washington, D.C.: National Academy of Sciences Press, 2000.

May, R.M., J.H. Lawton and N.E. Stork. "Assessing Extinction Rates." In *Extinction Rates*. Ed. J.H. Lawton and R.M. May. 1–24. Oxford University Press: 1995.

Nee, S. and R.M. May. "Extinction and the Loss of Evolutionary History." Science, 278 (1997), 692-694.

Sepkoski, J.J. "Phylogenetic and Ecologic Patterns in the Phanerozoic History of Marine Biodiversity." In Systematics, Ecology, and the Biodiversity Crisis. Ed. N. Eldredge. 77–100. New York: Columbia University Press, 1992.

Solow, A.R., L.A. Mound and K.J. Gaston. "Estimating the Rate of Synonymy." Syst. Biol, 44 (1995), 93–96.
Vane-Wright, R.I., C.J. Humphries and P.H. Williams. "What to Protect: Systematics and the Agony of Choice." Biol. Conserv., 55 (1991), 235–254.

Wilson, E.O. The Diversity of Life. Cambridge, Mass: Harvard University Press, 1992.

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).

	Geographic distribution				
Local population size		Wide t 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.

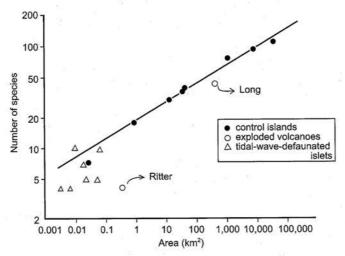


Figure 1. An example of the relation between species number and island area in an archipelago: number of resident, nonmarine, lowland bird species S on islands in the Bismarck Archipelago, plotted as a function of island area on a double logarithmic scale. The solid circles represent relatively undisturbed islands, and the straight line $S = 18.9 A^{0.18}$ 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?

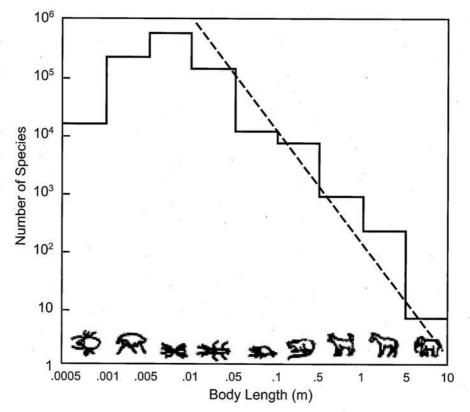


Figure 2. A crude estimate of the distribution of all terrestrial animals categorized according to characteristic length L. The dashed line indicates the relation $S - L^{-2}$, as in Fig. 3 (S = number of species). (After May, 1978)

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.

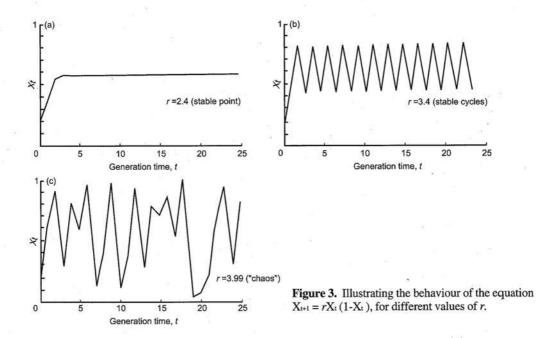
Connections Among Seemingly Different Questions. To illustrate how the above questions are intimately entwined with seemingly simpler questions of how many species there are on earth, consider the relation between foodweb patterns and global species numbers. If we really had a fundamental understanding 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.



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 microorganismns 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).

	Animals				
	Plants	Vertebrates	Invertebrates	Microorganisms	Fossils
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.

Group	Hammond (1995)	May (1999)
Protozoa	40	40
Algae	40	40
Plants	270	270
Fungi	70	70
Animals	1,320	<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

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

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.

		Hammond (1995)		
Group	High –	low	Working Figure	May (1999)
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
Verts	55 -	50	50	50
Nematodes	1,000 -	100	400	500
Molluscs	200 -	100	200	120
Arthropods	100,000 -	2,400	8,900	4,650
(crust)	(200 -	75)	(150)	(150)
(arachnids)	(1,000 -	300)	(750)	(500)
(insects)	(100,000 -	2,000)	(8,000)	(4,000)
others	800 -	200	250	250
Total	100,000 -	3,500	12,200	6,800
Range		100 - 3	million	
Plausible rar	iae :	15 - 5		178
Best guess	ige :	7	million	

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

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.

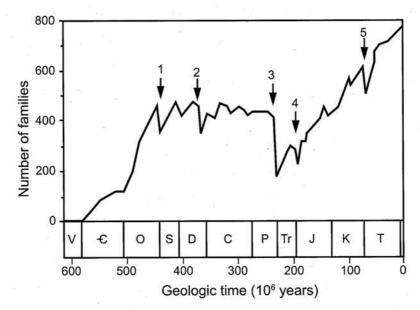


Figure 4. The history of the diversity of marine animal families, as shown by the fossil record over time. The curve connects 77 discrete data points, each giving the total number of well-skeletonized families from a particular stratigraphic stage. The arrows indicate the Big Five episodes of mass extinction. The length of the various geological epochs are indicated on the time axis (V, Vendian; \leftarrow , 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 e	t al (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
Cenzoic mammals	Raup and Stanley (1978)	1 – 2
Diatoms	Van Valen (1973)	8
Dinoflagellates	Van Valen (1973)	13
Planktinic 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		
Silurian graptolites	Koren and Rickards (1996)	0.2
Cambrian trilobites	Davidek et al, 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 et al, (1996)	0.2 - 7
- 1 2000-0010-001		(average 4)
Forams	Buzas and Culver (1984)	14 – 16
Coccoliths	J.R. Young, pers. comm.	c. 10
6 0		

Recent Extinctions. Over the past century, rigorously documented extinctions in wellstudied 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 10⁴ years. Although seemingly long, this is shorter by a factor of order 10⁻² to 10⁻³ than the background average lifespan of 10⁶ to 10⁷ 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 abovementioned 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 10² to 10³ 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.

REFERENCES

Diamond, J.M. 1974. "Colonization of Exploded Volcanic Islands by Birds." Science, 184, 803-806.

Fenchel, T. 1993. There are More Small than Large Species? Oikos, 68, 375-378.

Gaston, K.J. 1994. Rarity. Chapman and Hall; London.

Gaston, K.J. and E. Hudson. 1994. "Regional Patterns of Diversity and Estimates of Global Insect Species Richness." *Biodv. and Consv.*, **3**, 493-500.

Gaston, K.J. and May, R.M. 1992. "The Taxonomy of Taxonomists." Nature, 356, 281-282.

Grassle, J.F. and N.J. Maciolek. 1992. "Deep-Sea Species Richness: Regional and Local Diversity Estimates from Quantitative Bottom Samples." Amer. Natur. 139, 313–341.

Hammond, P.M. 1995. "The Current Magnitude of Biodiversity." In Global Biodiversity Assessment (ed. V.H. Heywood). 113–128. Cambridge Univ. Press; Cambridge.

Hawksworth, D.L. 1991. "The Fungal Dimension of Biodiversity: Magnitude, Significance and Conservation."

Mycol. Res., 95, 441-456.

HMSO. 1992. This Common Inheritance: Britain's Environment Strategy. HMSO; London.

McCann, K., A. Hastings, and G.R. Huxel, 1998. "Weak Trophic Interactions and the Balance of Nature, 395, 794–798.

McKinney, M.L. 1998. "Branching Models Predict Loss of Many Bird and Mammal Orders within Centuries." Anim. Consv., 1, 159–164.

Mace, G.M. 1994. "An Investigation into Methods for Categorizing the Conservation Status of Species." In Large Scale Ecology and Conservation Biology (eds. P.J. Edwards, R.M. May and N.R. Webb). 295-314. Blackwell; Oxford.

May, R.M. 1973. Stability and Complexity in Model Ecosystems. Princeton University Press; Princeton, N.J.

May, R.M. 1974. "Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, Chaos." Science, 186, 645–647.

May, R.M. 1976. "Simple Mathematical Models with Very Complicated Dynamics." Nature, 262, 459-467.

May, R.M. 1978. "The Dynamics and Diversity of Insect Faunas." In Diversity of Insect Faunas (eds. L.A. Mound and N. Waloff). 188–204. Blackwell; Oxford.

May, R.M. 1985. "When Two and Two Do Not Make Four: Nonlinear Phenomena in Ecology." The Croonian Lecture. Proc. Roy. Soc., B228, 241–266.

May, R.M. 1990. "How Many Species?" Phil. Trans. Roy. Soc., B330, 292-304.

May, R.M. 1994. "Conceptual Aspects of the Quantification of the Extent of Biological Diversity." Phil. Trans. Roy. Soc., B345, 13–20.

May, R.M. 1999." The Dimensions of Life on Earth." In *Nature and Human Society*. National Academy of Sciences Press; Washington, DC.

May, R.M., J.H. Lawton, and N.E. Stork, 1995. "Assessing Extinction Rates." In *Extinction Rates* (eds. J.H. Lawton and R.M. May). 1–24. Oxford University Press; Oxford.

May, R.M. and M.P.H. Stumpf, 2000. "Species Area Relations in Tropical Forests." *Science*, **290**, 2084–2086. Naeem, S. and S. Li, 1997. "Biodiversity Enhances Ecosystem Reliability." *Nature*, **390**, 507–509.

Nee, S. and R.M. May. 1997. "Extinction and the Loss of Evolutionary History." Science, 278, 692-694.

Pimm, S.L., J.H. Lawton, and J.E. Cohen, 1991." Food Web Patterns and their Consequences." Nature, 350, 660-674.

Rabinowitz, D., Cairns, S. and Dillon, T. 1986. "Seven Forms of Rarity." In Conservation Biology (ed. M.E. Soule). 182–204. Sinauer; Sunderland, Mass.

Sepkoski, J.J. 1992. "Phylogenetic and Ecologic Patterns in Phanerozoic History of Marine Biodiversity." In Systematics, Ecology, and the Biodiversity Crisis (ed. N. Eldredge). 77–1000. Columbia University; New York.

Solow, A.R., L.A. Mound, and K.J. Gaston, 1995. "Estimating the Rate of Synonymy." Syst. Biol, 44, 93-96.

Tilman, D., D. Wedon, and J. Knops, 1996. "Productivity and Sustainability Influenced by Biodiversity in Grassland Ecosystems." *Nature*, 379, 718–720.

Tilman, D., C.L. Lehman, and C.E. Bristow, 1998. "Diversity-Stability Relationships: Statistical Inevitability or Ecological Consequence?" Nature, 151, 277–282.

Vane-Wright, R.I., C.J. Humphries, and P.H. Williams, 1991. "What to Protect: Systematics and the Agony of Choice." Biol. Conserv., 55, 235–254.

Walter, K.S. and H.J. Gillett, eds. 1997. IUCN Red List of Threatened Plants. IUCN, Cambridge.

Wilson, E.O., ed. 1988. Biodiversity. National Academy of Press; Washington DC.

Major Publications

Lord (Robert) May of Oxford

Books

- May, R.M. Stability and Complexity in Model Ecosystems. Princeton: Princeton Univ. Press, 1973.
- —. Stability and Complexity in Model Ecosystems. Second Edition. Princeton: Princeton Univ. Press, 1974. Re-issued in the Princeton Landmarks in Biology series with a new Introduction, 2001, xi -xxxiv.
- May, R.M., ed. *Theoretical Ecology: Principles and Applications*. Oxford: Blackwell Scientific Publications, and Philadelphia: Saunders, 1976.
- —. Theoretical Ecology: Principles and Applications. Second Edition. Oxford: Blackwell Scientific Publications, and Sunderland, Mass.: Sinauer, 1981. (Translated into German, 1982. Translated into Chinese, 1983.)
- Anderson, R.M. and R.M. May, ed. Population Biology of Infectious Diseases. Berlin and N.Y.: Springer Verlag, 1982.

May, R.M., ed. Exploitation of Marine Communities. Berlin and N.Y.: Springer Verlag, 1984.

- Roughgarden, J., R.M. May and S.A. Levin, ed. *Perspectives in Ecological Theory*. Princeton: Princeton Univ. Press, 1989.
- Hassell, M.P. and R.M. May, ed. *Population Regulation and Dynamics*. London: The Royal Society, and Cambridge: Cambridge Univ. Press, 1990.
- Anderson, R.M. and R.M. May. Infectious Diseases of Humans: Dynamics and Control. Oxford: Oxford Univ. Press, 1991.
- Anderson, R.M. and R.M. May. Infectious Diseases of Humans: Dynamics and Control. Oxford: Oxford Univ. Press, 1991. Second printing with minor revisions in paperback, 1992.
- Beddington, J.R., D.H. Cushing, R.M. May and J.H. Steele, ed. Generalizing across Marine and Terrestrial Ecology. London: The Royal Society, 1994.
- Edwards, P.J., R.M. May and N.R. Webb, ed. *Large-Scale Ecology and Conservation Biology*. Oxford: Blackwell Scientific Publications, 1994.
- Grenfell, B. and R.M. May and H. Tong, ed. *Chaos and Forecasting*. London: The Royal Society (Single Issue of Philosophical Transactions, 348, No. 1688), 1994, 323–514. [Also published by World Scientific Publishing, Singapore, 1995.]

Lawton, J.H. and R.M. May, ed. Extinction Rates. Oxford: Oxford Univ. Press, 1995.

- Magurran, A.E. and R.M. May, ed. Evolution of Biological Diversity. Oxford: Oxford Univ. Press, 1999.
- Nowak, M.A. and R.M. May. Virus Dynamics: Mathematical Principles of Immunology and Virology. Oxford: Oxford Univ. Press, 2000.

Chapters in Books

- May, R.M. "Ecosystems: The First Three Billion Years and the Next Fifty Years." In *Brain Mechanism* and the Control of Behaviour. Ed. Messell and S.T. Butler. 65–119. Sydney: Shakespeare Head Press, 1972.
- --- "Stability in Model Ecosystems." In Proc. of the Ecological Society of Australia, 6, 18-56. 1971.
- —. "Ecosystems Pattern in Randomly Fluctuating Environments." In Progress in Theoretical Biology. Ed. R. Rosen and F. Snell. Vol. III, 1–50. N.Y.: Academic Press, 1974.
- —. "General Introduction." In *Ecological Stability*. Ed. M.B. Usher and M. Williamson. 1–14. London: Chapman and Hall. 1974.
- -... "How Many Species: Some Mathematical Aspects of the Dynamics of Populations." In Some

Mathematical Problems in Biology, Vol. 6. Ed. J. Cowan. 64–98. Providence, R.I.: American Mathematical Society, 1974.

- —. May, R.M. "Patterns of Species Abundance and Diversity." In Ecology and Evolution of Communities. Ed. J. Diamond and M. Cody. 81–120. Cambridge, Mass.: Harvard Univ. Press, 1975.
- —. May, R.M. "Stability in Ecosystems: Some Comments." In Unifying Concepts in Ecology. Plenary session reports at the First International Congress on Ecology. Ed. W.H. van Dobben and R.H. Lowe-McConnell. 161–168. The Hague: W. Junk Pubs, 1975.
- —. "Mathematical Aspects of the Dynamics of Animal Populations." In *Studies in Mathematical Biology*, MAA Studies in Mathematics, No. 15–16. Ed. S.L. Levin. 317–366. Washington, D.C.: Mathematical Association of America, 1978.
- —. "Mathematical Models and Ecology: Past and Future." In *The Changing Scenes in the Natural Sciences*, 1776–1976. Ed. C.E. Goulden. 189–201. Philadelphia: Academy of Natural Sciences, 1977.
- —. "Factors Controlling the Stability and Breakdown of Ecosystems." In *The Breakdown* and *Restoration of Ecosystems*. Ed. M.W. Holdgate and M.J. Woodman. 11–25. N.Y.: Plenum Press, 1978.
- —. "The Dynamics and Diversity of Insect Faunas." In *Diversity of Insect Faunas*. Ed. L.A. Mound and N. Waloff. 188–204. Oxford: Blackwell Scientific Publications, 1978.
- —. "The Structure and Dynamics of Ecological Communities." In *Population Dynamics*. Ed. R.M. Anderson, B.D. Turner and L.R. Taylor. 385–407. Oxford: Blackwell Scientific Publications, 1979.
- Aron, J.L. and R.M. May. "The Population Dynamics of Malaria." In *Population Dynamics of Infectious Diseases*. Ed. R.M. Anderson. 139–179. London: Chapman and Hall, 1982.
- May, R.M. "Mathematical Models in Whaling and Fisheries Management." In Some Mathematical Questions in Biology, Vol. 13. Ed. G.F. Oster. 1–64. Providence, R.I: American Mathematical Society, 1980.
- —. "The Dynamics of Natural and Managed Populations." In Mathematical Theory of the Dynamics of Populations II. Ed. R.W. Hiorns and D. Cooke. 5–29. N.Y.: Academic Press, 1981.
- —. "Modelling Recolonisation by Neotropical Migrants in Habitats with Changing Patch Structure, with Notes on the Age Structure of Populations." In *Forest Island Dynamics in Man-Dominated Landscapes*, Vol. 41. Ed. R.L. Burgess and D.N. Sharpe. In *Springer-Verlag Series on Ecological Studies*. 207–213. N.Y.: Springer Verlag, 1981.
- —. "Population Biology of Parasitic Infections." In *The Current Status and Future of Parasitology*. Ed. K. S. Warren and E. F. Purcell. 208–235. N.Y.: Josiah Macy, Jr., Foundation, 1981.
- May, R.M. and J.R. Beddington. "Notes on Some Topics in Theoretical Ecology, in Relation to the Management of Locally Abundant Populations of Mammals." In *Problems in Management of Locally Abundant Wild Mammals*. Ed. P.A. Jewell and S.J. Holt. 205–216. N.Y.: Academic Press, 1982.
- Martin, R.D. and R.M. May. "Outward Signs of Breeding." In Evolution Now: A Century after Darwin. Ed. J. Maynard Smith. 234–239. London: Macmillan, 1982.
- May, R.M. and R.M. Anderson. "Parasite-Host Coevolution." In *Coevolution*. Ed. D.J. Futuyma and M. Slatkin. 186–206. Sunderland, Mass.: Sinauer, 1983.
- May, R.M. "Nonlinear Problems in Ecology and Resource Management." In *Chaotic Behaviour of Deterministic Systems*. Ed. G. Iooss, R.H.G. Helleman and Stora. 389–439. Amsterdam: North-Holland Publishing, 1983.
- —. "Parasitism: Ecology and Population Biology." In *Tropical and Geographical Medicine*. Ed. K.S. Warren and A.A.F. Mahmoud. 152–166. N.Y.: McGraw-Hill, 1984.
- —. "Creation, Evolution, and High School Texts." In Science and Creationism. Ed. A. Montagu. 306–310. Oxford: Oxford Univ. Press, 1984.
- ---. "Adaptations, Constraints and Patterns of Evolutions." In Evolution: Essays in Appreciation of John

Maynard Smith. Ed. D.J. Greenwood, M. Slatkin and P.H. Harvey. 107–116. Cambridge: Cambridge Univ. Press, 1984.

- —. May, R.M. "An Overview: Real and Apparent Patterns in Community Structure." In *Ecological Communities Conceptual Issues and the Evidence*. Ed. D.R. Strong, D. Simberloff, L.G. Abele and A.B. Thistle. 1–16. Princeton: Princeton Univ. Press, 1984.
- May, R.M. and D.I. Rubenstein. "Mammalian Reproductive Strategies." In *Reproduction in Mammals*, Vol. 4. Ed. C.R. Austin and R.V. Short. 1–23. Cambridge: Cambridge Univ. Press, 1985.
- Hassell, M.P. and R.M. May. "From Individual Behaviour to Population Dynamics." In *Behavioural Ecology*. Ed. R. Sibly and R. Smith. 3–32. Oxford: Blackwell Scientific Publications, 1985.
- May, R.M. "Host-Parasite Associations: Their Population Biology and Population Genetics." In Ecology and Genetics of Host-Parasite Interactions. Ed. D. Rollinson and R.M. Anderson. 243–262. N.Y.: Academic Press, 1985.
- —. "Population Dynamics." In *The Study of Populations*. Ed. H. Messel. 1–44 (4 chaps). Sydney: Pergamon Press, 1985.
- —. "Ecology of Insect-Pathogen Interactions, and Some Possible Applications." In Ecological Theory and Integrated Pest Management. Ed. M. Kogan. 185–201. N.Y.: John Wiley & Sons, 1986.
- Dobson, A.P. and R.M. May. "Patterns of Invasions by Pathogens and Parasites." In *Ecological Biological Invasions of North America and Hawaii*. Ed. H.A Mooney and J.A. Drake. 58–76. N.Y.: Springer Velag, 1986.
- May, R.M. "Experimental Control of Malaria in West Africa." In Ecological Knowledge and Environmental Problem-Solving: Concepts and Case Studies (NAS Committee on Applications of Ecological Theory to Environmental Problems). 191–203. Washington, D.C.: National Academy Press, 1986.
- Dobson, A.P. and R.M. May. "Population Dynamics and the Rate of Evolution of Pesticide Resistance." In *Pesticide Resistance: Strategies and Tactics for Management* (NAS Committee on Strategies for the Management of Pesticide Resistance Pest Populations). 170–193. Washington, D.C.: National Academy Press. 1986.
- —. "Disease and Conservation." In Conservation Biology: The Science of Scarcity and Diversity. Ed. M.E. Soule. 345–365. Sunderland, Mass.: Sinauer, 1986.
- May. R.M. "Population Biology of Microparasitic Infections." In *Mathematical Ecology: An Introduction*. Ed. T.G. Hallam and S.A. Levin. 405–442. N.Y.: Springer Verlag, 1986.
- Dobson, A.P. and R.M. May. "The Effects of Parasites on Fish Populations: Theoretical Aspects." In Parasitology Quo Vadit? Ed. N.J. Howell. 363–370. Canberra: Australian Academy of Science, 1986.
- May, R.M. "Mathematical Models in Ecology: The Dynamics of Surprise." In *Highlights in Science*. Ed. H. Messel. 88–128. Sydney: Pergamon Press, 1987.
- —. "Prolog." In Size-Structured Populations. Ed. B. Ebenman and L. Persson. 1–3. Berlin: Spring-Verlag, 1988.
- May, R.M., R.M. Anderson and A.M. Johnson. "Patterns of Infectiousness and the Transmission of HIV-1." In AIDS 1988: AAAS Symposia Papers. Ed. R. Kulstad. 75–83. Washington, D.C.: American Association for the Advancement of Science, 1988.
- Hassell, M.P. and R.M. May. "The Population Biology of Host-Parasite and Host-Parasitoid Associations." In *Perspectives in Ecological Theory*. Ed. J. Roughgarden, R.M. May and A. Levin. 319–347. Princeton: Princeton Univ. Press, 1989.
- May, R.M. "How Many Species?" In *The Fragile Environment: The Darwin College Lectures*. Ed. L.E. Friday and R.A. Laskey. 61–81. Cambridge: Cambridge Univ. Press, 1989. (Reprinted in Italian as "Il Fragile Ambiente" by Edizioni Dedalo, 1991.)
- —. "Levels of Organization in Ecology." In *Ecological Concepts*. British Ecological Society's Jubilee Symposium. Ed. J.M. Cherrett. 339–363. Oxford: Blackwell Scientific Publications, 1989.

- --. "Parasitism: Ecology and Population Biology." In *Tropical and Geographical Medicine*, 2nd Edition. Ed. K.S. Warren and A.A.F. Mahmoud. 130-145. N.Y.: McGraw-Hill, 1989.
- Anderson, R.M. and R.M. May. "Complex Dynamical Behaviour in the Interaction between HIV and the Immune System." In *Cell to Cell Signalling*. Ed. A. Goldbeter. 335–349. London: Academic Press, 1989.
- May, R.M., R.M. Anderson and A.R. McLean. "Possible Demographic Consequences of HIV/AIDS Epidemics: II, Assuming HIV Infection Does Not Necessarily Lead to AIDS." In *Mathematical Approaches to Problems in Resource Management and Epidemiology*. Lecture Notes in Biomathematics, Vol. 81. Ed. C. Castillo-Chauvez, S.A. Levin and C.A. Shoemaker. 220–245. N.Y.: Springer Verlag, 1989.
- May, R.M. and R.M. Anderson. "Heterogenities, Cofactors and Other Aspects of the Transmission Dynamics of HIV/AIDS." In *Current Topics in AIDS*, Vol. 2. Ed. M.S. Gottlieb, et al. 33–67. N.Y.: John Wiley & Sons, 1989.
- —. "The Transmission Dynamics of Human Immunodeficiency Virus." In Applied Mathematical Ecology (Biomathematics, Vol. 18). Ed. S.A. Levin, T.G. Hallam and L. Gross. 263–311. N.Y.: Springer Verlag, 1989.
- May, R.M. and T.R.E. Southwood. "Introduction." In *Living in a Patchy Environment*. Ed. B. Shorrocks and I.R. Swingland. 1–22. Oxford: Oxford Univ. Press, 1990.
- May, R.M. "Population Biology and Population Genetics of Plant-Pathogen Associations." In Pests, Pathogens and Plant Communities. Ed. J.J. Burdon and S.R. Leather. 309–325. Oxford: Blackwell Scientific Publications, 1990.
- Dobson, A.P. and R.M. May. "Parasites, Cuckoos, and Avian Population Dynamics." In *Bird Population Studies*. Ed. C.M. Perrins, J.D. Lebreton and G.J.M. Hirons. 391–412. Oxford: Oxford Univ. Press, 1991.
- May, R.M. "The Dynamics and Genetics of Host-Parasite Associations." In Parasite-Host Associations: Coexistence or Conflict? Ed. C.A. Toft, A. Aeschlimann and L. Bolis. 102–128. Oxford: Oxford Univ. Press, 1991.
- —. "How Many Species on Earth Today? And Tomorrow? How Do We Manage the Ark?" Chap. 2,3,4. In *Living with the Environment*. Ed. L.E. Cram and D.D. Millar. 8–35. Sydney & Oxford: Pergamon, 1991.
- —. "The Role of Ecological Theory in Planning Re-Introduction of Endangered Species." In Beyond Captive Breeding: Re-Introducing Endangered Mammals to the Wild. Ed. J.H.W. Gipps. 145–163. Oxford: Oxford Univ. Press, 1991.
- May, R.M., S. Nee and C.H. Watts. "Could Intraspecific Brood Parasitism Cause Population Cycles?" In Acta XX Congressus Internationalis Ornithologici, Vol. II. Ed. B.D. Bell, et al. 1012–1022. Wellington, NZ: NZ Ornithological Congress Trust Board, 1991.
- May, R.M. "Past Efforts and Future Prospects towards Understanding How Many Species There Are." In *Biodiversity and Global Change*. Ed. O.T. Solbrig, H.M. van Emden and P.G.W.J. van Oordt. 71–81. Paris: International Union of Biological Sciences, 1992.
- May, R.M. and Watts, C.H. "The Dynamics of Predator-Prey and Resource-Harvester Systems." In Natural Enemies: The Population Biology of Predators, Parasites and Diseases. Ed. M.J. Crawley. 431–457. Oxford: Blackwell Scientific Publications, 1992.
- Futuyma, D.J. and R.M. May. "The Coevolution of Plant-Insect and Host-Parasite Relationships." In Genes in Ecology. Ed. R.J. Berry, T.J. Crawford and G.M. Hewitt. 139–166. Oxford: Blackwell Scientific Publications, 1992.
- May, R.M. "The Chaotic Rhythms of Life." In *The New Scientist Guide to Chaos.* Ed. N. Hall. 82–95. London: Penguin Books, 1991. (Published in the USA as *Exploring Chaos.* N.Y.: Norton, 1993.)
- —. "The Modern Biologist's View of Nature." In *The Concept of Nature*. Ed. J. Torrance. 167–182. Oxford: Oxford Univ. Press, 1993.

- —. "Ecology and Evolution of Host-Virus Associations." In *Emerging Viruses*. Ed. S.S. Morse. 58–68. Oxford: Oxford Univ. Press, 1993.
- Holton, D. and R.M. May, "Chaos and One-Dimensional Maps (Ch. 5); Models of Chaos from Natural Selection (Ch. 6); Distinguishing Chaos from Noise (Ch. 7); The Chaos of Disease Response and Competition (Ch. 8)." In *The Nature of Chaos*. Ed. T. Mullin. 95–200. Oxford: Oxford Univ. Press, 1993.
- May, R.M. "Biological Diversity: Britain's Traditions and Their Implications." In Action for Biodiversity in the UK. Ed. F.J. Wright, C.A. Galbraith and R. Bendall. 16–20. Peterborough: JNCC Publications Branch, 1993.
- —. "Global Change: The Need and Concern for Collecting and Preserving." In Proc. of the International Symposium and First World Congress on the Preservation and Conservation of Natural Collections, Vol. 3. Ed. C.L. Rose, S.L. Williams and J. Gisbert. 35–42. Madrid: Spanish Ministry of Culture, 1993.
- —. "The Effects of Spatial Scale on Ecological Questions and Answers." In Large-Scale Ecology and Conservation Biology. Ed. P.J. Edwards, R.M. May and N.R. Webb. 1–17. Oxford: Blackwell Scientific Publications, 1994.
- Jones, T.M., M.P. Hassell and R.M. May. "Population Dynamics of Host-Parasitoid Interactions." In *Parasitoid Community Ecology*. Ed. A. Hawkins and W. Sheenhan. 371–394. Oxford: Oxford Univ. Press, 1994.
- May, R.M. "Changing Diseases in Changing Environments." In *Health and the Environment*. Ed. B. Cartledge. 151–171. Oxford: Oxford Univ. Press, 1994.
- May, R.M., J.H. Lawton and N.E. Stork. "Assessing Extinction Rates." In *Extinction Rates*. Ed. J.H. Lawton and R.M. May. 1–24. Oxford: Oxford Univ. Press, 1995.
- Nee, S., E.C. Holmes, R.M. May and P.H. Harvey. "Estimating Extinction from Molecular Phylogenies." In *Extinction Rates*. Ed. J.H. Lawton and R.M. May. 164–182. Oxford: Oxford Univ. Press, 1995.
- May, R.M. "Spatial Chaos and Its Role in Ecology and Evolution." In *Frontiers in Mathematical Biology* (Lecture Notes in Biomathematics, Vol. 100). Ed. S.A. Levin. 326–344. N.Y.: Springer-Verlag, 1995.
- May, R.M., S. Bohoeffer and M.A. Nowak. "Spatial Games and Evolution of Cooperation." In Advances in Artificial Life. Ed. F. Morán, A. Moreno, J.J. Merelo and P. Chacón. 749–759. Berlin: Springer-Verlag, 1995.
- —. "Fractals, Chaos and Strange Attractors (from programme notes for Stoppard's play, Arcadia)." In The Faber Book of Science. Ed. J. Carey. 495–504. London: Faber & Faber, 1995.
- —. "The Co-Evolutionary Dynamics of Viruses and Their Hosts." In Molecular Basis of Virus Evolution. Ed. A. Gibbs, C.H. Calisher and F. García-Arenal. 192–212. Cambridge: Cambridge Univ. Press, 1995.
- —. "Introduction." In Aspects of the Genesis and Maintenance of Biological Diversity. Ed. M.A. Hochberg, J. Clobert and R. Barbault. 1–13. Oxford: Oxford Univ. Press, 1996.
- Nee, S., May, R.M. and M.P. Hassell. "Two Species Metapopulation Models." In *Metapopulation Biology: Ecology, Genetics and Evolution*. Ed. I Hanski and M. Gilpin. 123–147. USA.: Academic Press, 1997.
- May, R.M. "Introductory and Concluding Remarks." In *Multitrophic Interactions in Terrestrial Systems*. Ed. A.C. Gange and V.K. Brown. 305–306, 419–421. Oxford: Blackwell Science Publications, 1997.
- —. Foreword in *The Role of Genetics in Conserving Small Populations*. Ed. T.E. Tew, T.J. Crawford, J.W. Spencer, D.P. Stevens, M.B. Usher and J. Warren. 5–6. Hertford: Stephen Austin & Sons (for JNCC), 1997.

-... "Life Science." In Science and Society, a JSPS-UK Research Council Symposium 1995. 129-130.

Northampton: Pilkington Press, 1997.

- —. "The Fractal Frontiers of Science." In Nurturing Creativity in Research: Ideas as the Foundations of Innovation. Ed. P.M. Shearmur, C.B. Osmond and P. Pockley. 136–142. Canberra: Australian National Univ. Press, 1997.
- Ferguson, N.M., R.M. May and R.M. Anderson. "Measles: Persistence and Synchronicity in Disease Dynamics." In Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions. Ed. D. Tilman and P. Kareiva. 137–157. Princeton: Princeton Univ. Press, 1997.
- May, R.M. "Levels of Organization in Ecological Systems." In *The Limits of Reductionism in Biology*. Ed. G.R. Bock and J.A. Goode. 193–202. Chichester: John Wiley & Sons, 1998.
- —. "Ecology in Practice." In Ecology: Theories and Applications. Ed. P. Stiling. 470–471. New Jersey: Prentice Hall, 1998.
- —. "The European Dimension of the UK Science Base: Patterns and Policies." In Science Funding, The European Dimension. 61–66. Discussion Meeting of The Royal Society, 17 March, 1998.
- May, R.M. and K. Tregonning. "Global Conservation and UK Government Policy." In Conservation in a Changing World. Ed. G.M. Mace, A. Balmford and J.R. Ginsberg. 287–301. Cambridge: Cambridge Univ. Press, 1998.
- May, R.M. "What We Do and Do Not Know about the Diversity of Life on Earth." In Perspectives in Ecology. Ed. A. Farina. 33–40. Leiden, NL: Backhuys Pubs., 1998.
- —. "Are We Getting Better at Exploiting Our Scientific and Innovative Capability?" In RSA on Design and Innovation, 97–113. Aldershot: Gower, 1999.
- —. "Conservation: Dealing with Extinction." In *Imagine Tomorrow's World*. Ed. J.A. McNeely. 57–68. Gland, Switzerland: The International Union for Conservation of Nature (IUCN), 1999.
- —. "Science Advice, Social Responsibility and Policy-Making." In Science, Technology and Social Responsibility. Ed. L. Wolpert. 91–95. London: The Royal Society, 1999.
- —. "The Dimensions of Life on Earth." In Nature and Human Society, The Quest for a Sustainable World. Ed. P.H. Raven. 30–45. Washington, D.C.: US National Academy Press, 2000.
- May, R.M. and R. Pitts. "Communicating the Science behind Global Environmental Change Issues." In The Daily Globe Environmental Change, the Public and the Media. Ed. J. Smith. 15–25. London: Earthscan Pubs., 2000.
- May, R.M. "The Scientific Approach to Complex Systems." In World Conference on Science. Ed. A.M. Cetto. 63–65. UNESCO, 2000.

Articles

May, R.M. "Stability in Multispecies Community Models." Math. Biosc., 12 (1971), 59-79.

Kramer, N.F. and R.M. May. "Interspecific Competition, Predation and Species Diversity: A Comment." J. Theor. Biol., 34 (1972), 289–293.

—. "What is the Chance that a Large Complex System will be Stable?" *Nature*, 238 (1972), 413–414.
—. "Limit Cycles in Prey-Predator Communities." *Science*, 177 (1972), 900–902.

- May, R.M. and R.H. MacArthur. "Niche Overlap as a Function of Environmental Variability." Proc. Nat. Acad. Scis., 69 (1972), 1109–1113.
- May, R.M. "Time-Delay Versus Stability in Population Models with Two and Three Trophic Levels." Ecology, 54 (1973), 315–325.

Hassell, M.P. and R.M. May. "Stability in Insect Host-Parasite Models." J. Anim. Ecol., 42 (1973), 693–726.

- May, R.M. "On Relationships between Various Types of Population Models." Amer. Naturl., 107 (1973), 46–57.
- -... "Mass and Energy Flow in Closed Ecosystems: A Comment." J. Theor. Biol., 39 (1973), 155-163.

-. "Qualitative Stability in Model Ecosystems." Ecology, 54 (1973), 638-641.

- -. "Stable Limit Cycles in Predator-Prey Populations: A Comment." Science, 181 (1973), 1074.
- —. "Stability in Randomly Fluctuating versus Deterministic Environments." Amer. Naturl., 107 (1973), 621–650.
- -. "On the Theory of Niche Overlap." Theor. Pop. Biol., 5 (1974), 297-332.
- Hassell, M.P. and R.M. May. "Aggregation of Predators and Insect Parasites and its Effect on Stability." J. Anim. Ecol., 43 (1974), 567–594.
- May, R.M., G.R. Conway, M.P. Hassell and T.R.E. Southwood. "Time Delays, Density Dependence and Single-Species Oscillations." J. Anim. Ecol., 43 (1974), 747–770.
- Southwood, T.R.E., R.M. May, M.P. Hassell and G.R. Conway. "Ecological Strategies and Population Parameters." Amer. Naturl., 108 (1974), 791–804.
- May, R.M. "Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, Chaos." Science, 186 (1974), 645–647.
- May, R.M. and W.J. Leonard. "Nonlinear Aspects of Competition between Three Species." SIAM J. Appl. Math. 29 (1975), 243–253.

May, R.M. "Some Notes on Estimating the Competition Matrix." Ecology, 56 (1975), 737-741.

- —. "Biological Populations Obeying Difference Equations: Stable Points, Stable Cycles, and Chaos." J. Theor. Biol., 51 (1975), 511–524.
- May, R.M., J.A. Endler and R.E. McMurtrie. "Gene Frequency Clines in the Presence of Selection Opposed by Gene Flow." Amer. Naturl., 109 (1975), 659–676.
- May, R.M. "Change in Gene Frequency under Selection in a Finite Population: A Comment." Theor. Pop. Biol., 7 (1975), 208–211.
- Beddington, J.R. and R.M. May. "Time Delays are Not Necessarily Destabilising." Math. Biosc., 27 (1975), 109–117.

May, R.M. "A Note on Random Sets Mosaics." J. Math. Biol., 2 (1975), 351-357.

- May, R.M. and G.F. Oster. "Bifurcations and Dynamic Complexity in Simple Ecological Models." Amer. Naturl., 110 (1976), 573–599.
- Hassell, M.P., J.H. Lawton and R.M May. "Patterns of Dynamical Behaviour in Single-Species Populations." J. Anim. Ecol., 45 (1976), 471–486.
- Levin, S.A. and R.M. May. "A Note on Difference-Delay Equations." *Theor. Pop. Biol.*, 9 (1976), 178–187.
- May, R.M. "Estimating: A Pedagogical Note." Amer. Naturl., 110 (1976), 496-499.
- —. "Simple Mathematical Models with Very Complicated Dynamics." *Nature*, 262 (1976), 459–467. [Reprinted:
- (i) Hungarian translation, published by Hungarian Academy of Sciences, Alkalmazott Matematikai Lapok, 8 (1982), 427–446.
- (ii) In Chaos. Ed. Hao Bai-Lin. Singapore: World Scientific Publishing, 1984.
- (iii) In Univ. in Chaos. Ed. P. Cvitanovic. Bristol: Adam Hilger, 1984.
- (iv) In Chaos, Vol. II. Ed. Hao Bai-Lin. Singapore: World Scientific Publishing, 1990.]

Diamond, J.R. and R.M. May. "Species' Turnover Rates on Islands: Dependence on Census Interval." Science, 197 (1977), 266–270.

- Beddington, J.R. and R.M. May. "Harvesting Natural Populations in a Randomly Fluctuating Environment." Science, 197 (1977), 463–465.
- May, R.M. "Togetherness among Schistosomes: Its Effect on the Dynamics of the Infection." Math. Biosc., 35 (1977), 301–343.
- Hamilton, W.D. and R.M. May. "Dispersal in Stable Habitats." Nature, 269 (1977), 578-581.
- Godley, W. and R.M. May. "The Macroeconomic Implications of Devaluation and Import Restriction." Econ. Pol. Rev., 3 (1977), 32–42.
- May, R.M. "Dynamical Aspects of Host-Parasite Associations: Crofton's Model Revisited." Parasitol., 75 (1977), 259–276.

 -. "Thresholds and Breakpoints: Ecosystems with a Multiplicity of Stable States." Nature, 269 (1977), 471–477.

- Bradley, D.J. and R.M. May. "Consequences of Helminth Aggregation for the Dynamics of Schistosomiasis." Trans. Roy. Soc. Trop. Med. & Hyg., 72 (1978), 262–273.
- Anderson, R.M. and R.M. May. "Regulation and Stability of Host-Parasite Population Interactions: (I) Regulatory Processes." J. Anim. Ecol., 47 (1978), 219–247.
- May, R.M. and R.M. Anderson. "Regulation and Stability of Host-Parasite Population Interactions: (II) Destabilising Processes." J. Anim. Ecol., 47 (1978), 249–267.
- May, R.M. "Host-Parasitoid Systems in Patchy Environments: A Phenomenological Model." J. Anim. Ecol., 47 (1978), 833–844.

-. "Evolution of Ecological Systems." Sci. Amer., 239 (1978), 160-175.

- May, R.M., J.R. Beddington, J.W. Horwood and J.G. Shepherd. "Exploiting Natural Populations in an Uncertain World." *Math. Biosci.*, 42 (1978), 219–252.
- May, R.M. "Bifurcations and Dynamic Complexity in Ecological Models." Annals NY Acad. Scis., 316 (1979), 517–529.
- May. R.M. "Simple Models for Single Populations: An Annotated Bibliography." Firtchritte der Zool., 25 (1979), 95–107.
- Anderson, R.M. and R.M. May. "Prevalence of Schistosome Infections within Molluscan Populations: Observed Patterns and Theoretical Predictions." *Parasitol.*, 79 (1979), 63–94.
- May, R.M., J.R. Beddington, C.W. Clark, S.J. Holt and R.M. Anderson. "Laws, Management of Multispecies Fisheries." Science, 205 (1979), 267–277.
- Anderson, R.M. and R.M. May. "Population Biology of Infectious Diseases: Part I." Nature, 280 (1979), 361–367.
- May, R.M. and Anderson, R.M. "Population Biology of Infectious Diseases: Part II." Nature, 280 (1979), 455–461.
- Beddington, J.R. and R.M. May. "A Possible Model for the Effect of Adult Sex Ratio and Density on the Fecundity of Sperm Whales." Reports of the *International Whaling Commission*, Special Issue 2 (1980), 75–76. [Also issued as SC/S30/ 4 (1977).]
- May, R.M. and J.R. Beddington. "The Effect of Adult Sex Ratio and Density on the Fecundity of Sperm Whales." Reports of the *International Whaling Commission*, Special Issue 2 (1980), 213–217. [Also issued as SC/S78/14 (1978).]
- Comins, H.N., W.D. Hamilton and R.M. May. "Evolutionary Stable Dispersal Strategies." J. Theor. Biol., 82 (1980), 205–230.
- Beddington, J.R. and R.M. May. "Maximum Sustainable Yield in Systems Subject to Harvesting at More Than One Trophic Level." *Math. Biosc.*, 51 (1980), 261–281.
- Anderson, R.M. and R.M. May. "Infectious Diseases and Population Cycles of Forest Insects." Science, 210 (1980), 658–661.
- May, R.M. and G.F. Oster. "Period Doubling and the Onset of Turbulence: An Analytic Estimate of the Feigenbaum Ratio." Phys. Letts., A 78 (1980), 1–3.
- May, R.M. and M.P. Hassell. "The Dynamics of Multi-Parasitoid-Host Interactions." Amer. Naturl., 117 (1981), 234–261.
- May, R.M. "Nonlinear Phenomena in Ecology and Epidemiology." Annals NY Acad. Scis., 357 (1981), 267–281.
- Anderson, R.M. and R.M. May. "The Population Dynamics of Microparasites and Their Invertebrate Hosts." Phil. Trans. Roy. Soc. B., 291 (1981), 451–524.
- Anderson, R.M., H.C. Jackson, R.M. May and A.M. Smith. "Population Dynamics of Fox Rabies in Europe." Nature, 289 (1981), 765–771.
- Bonner, J.T. and R.M. May. "Introduction." To Charles Darwin, The Descent of Man. (First Edition, 1871). vii—xii. Paperback reprint, Princeton: Princeton Univ. Press, 1981.

May, R.M. "The Role of Theory in Ecology." Amer. Zool., 21 (1981), 903-910.

- May, R.M., M.P. Hassell, R.M. Anderson and D.W. Tonkyn. "Density Dependence in Host-Parasitoid Models." J. Anim. Ecol., 50 (1981), 855–865.
- Anderson, R.M. and R.M. May. "Directly Transmitted Infectious Diseases: Control by Vaccination." Science, 215 (1982), 1053–1060.
- [Also circulated, in an expanded form, as Report ICCET Series E, No. 2 (1981), by the Imperial College Centre for Environmental Technology.]
- —. "The Control of Communicable Diseases by Age-Specific Immunisation Schedules." Lancet, 16 January (1982), 160.

-. "Coevolution of Hosts and Parasites." Parasitol., 85 (1982), 411-426.

Beddington, J.R. and R.M. May. "Multispecies Harvesting in Natural Ecosystems." Sci. Amer., 247 (1982), 60–69.

- Anderson, R.M. and R.M. May. "The Population Dynamics and Control of Human Helminth Infections." Nature, 297 (1982), 557–563.
- -. "Vaccination and Herd Immunity." Lancet, 3 April (1982), 807.
- -... "The Logic of Vaccination." New Sci., 96 (1982), 410-415.
- May, R.M. "Parasitic Infections as Regulators of Animal Populations." Amer. Sci., 71 (1983), 36–45.
 —. "Vaccination against Rubella and Measles: Quantitative Evaluation of Different Policies." J. Hygiene, 90 (1983), 259–325.
- Hassell, M.P., J.K. Waage and R.M. May. "Variable Parasitoid Sex Ratios and Their Effect on Host-Parasitoid Dynamics." J. Anim. Ecol., 52 (1983), 889–904.
- Harvey, P.H., R.K. Colwell, J.W. Silvertown and R.M. May. "Null Models in Ecology." Ann. Rev. Ecol., Sys., 14 (1983), 189–211.
- May, R.M. and R.M. Anderson. "Epidemiology and Genetics in the Coevolution of Parasites and Hosts." Proc. Roy. Soc. B., 219 (1983), 281–313. [Reprinted in Mathematical Genetics Ed. W.F. Bodmer and J.F.C. Kingman. 61–93. London: The Royal Society, 1983.]
- Ehrlich, P.R., R.M. May, N. Myers, et al. "Long-Term Biological Consequences of Nuclear War." Science, 222 (1983), 1293–1300.
- Anderson, R.M. and R.M. May. "Two-Stage Vaccination Programme against Rubella." Lancet, 17 December, 1983. 1416–1417.
- May, R.M. and R.M. Anderson. "Spatial Heterogeneity and the Design of Immunisation Programmes." Math. Biosc., 72 (1984), 83–111.

Anderson, R.M., B.T. Grenfell and R.M. May. "Oscillatory Fluctuations in the Incidence of Infectious Disease and the Impact of Vaccination: Time Series Analysis." J. Hygiene, 93 (1984), 587–608.

- May, R.M. "Regulation of Populations with Non-Overlapping Generations by Microparasites: A Purely Chaotic System." Amer. Naturl., 125 (1985), 573–584.
- Ives, A.R. and R.M. May. "Competition within and between Species in a Patchy Environment: Relations between Microscopic and Macroscopic Models." J. Theor. Biol., 115 (1985), 65–92.
- Anderson, R.M. and R.M. May. "Spatial, Temporal, and Genetic Heterogeneity in Host Populations and the Design of Immunization Programmes." IMA J. Maths. Appl. in Med. & Biol., 1 (1985), 233–266.
- May, R.M. and S.K. Robinson. "Population Dynamics of Avian Brood Parasitism." Amer. Naturl., 126 (1985), 475–494.

May, R.M. "Ecological Aspects of Disease and Human Populations." Amer. Zool., 25 (1985), 441-450.

- Anderson R.M. and R.M. May. "Age-Related Changes in the Rate of Disease Transmission: Implications for the Design of Vaccination Programmes." J. Hygiene, 94 (1985), 365–436.
- —. "Herd Immunity to Helminth Infection and Implications for Parasite Control." Nature, 315 (1985), 493–496.
- —. "Helminth Infections of Humans: Mathematical Models, Population Dynamics and Control." Advances in Parasitol., 24 (1985), 1–104.

- May, R.M. and R.M. Anderson. "Endemic Infections in Growing Populations." Math. Biosc., 76 (1985), 1–16.
- Anderson, R.M. and R.M. May. "Vaccination and Herd Immunity to Infectious Diseases." Nature, 318 (1985), 323–329.

May, R.M. and J. Seger. "Ideas in Ecology: Yesterday and Tomorrow." Amer. Sci., 74 (1986), 256-267.

- Hassell, M.P. and R.M. May. "Generalist and Specialist Natural Enemies in Insect Predator-Prey Interactions." J. Anim. Ecol., 55 (1986), 923–940.
- Anderson, R.M., J.A. Crombie and R.M. May. "Predisposition to Helminth Infection in Man." Nature, 320 (1986), 195–196.
- May, R.M. "When Two and Two Do Not Make Four: Nonlinear Phenomena in Ecology." The Croonian Lecture, 1985. Proc. Roy. Soc. B., 228 (1986), 241–266.
- Anderson, R.M. and R.M. May. "The Invasion, Persistence and Spread of Infectious Diseases within Animal and Plant Communities." Proc. Roy. Soc. B., 314 (1986), 533–570.
- Anderson, R.M., R.M. May, G.F. Medley and A. Johnson. "A Preliminary Study of the Transmission Dynamics of the Human Immunodeficiency Virus (HIV), the Causative Agent of AIDS." IMA J. Maths. Appl. in Med. & Biol., 3 (1986), 229–263.
- May, R.M. "The Search for Patterns in the Balance of Nature: Advances and Retreats." The Robert H. MacArthur Award Lecture, 1985. Ecology, 67 (1986), 1115–1126.
- May, R.M. and R.M. Anderson. "Transmission Dynamics of HIV Infection." Nature, 326 (1987), 137-142.
- Anderson, R.M. and R.M. May. "Plotting the Spread of AIDS." New Sci., 26 March (1987), 54-59.
- Crawley, M.J. and R.M. May. "Population Dynamics and Plant Community Structure: Competition between Annuals and Perennials." J. Theor. Biol., 125 (1987), 475–489.
- May, R.M. "Epidemiology of AIDS." Family Health International (Special Issue), (1987), 4-5.
- —. "Chaos and the Dynamics of Biological Populations." Proc. Roy. Soc., A 413 (1987), 27–44. [Reprinted in Dynamical Chaos. Ed. M.V. Berry, I.C. Percival and N.O. Weiss. 27–44. London: The Royal Society, 1987.]
- —. "Nonlinearities and Complex Behaviour in Simple Ecological and Epidemiological Models." Ann. NY Acad. Scis., 504 (1987), 1–15. [Reprinted in Perspectives in Biological Dynamics and Theoretical Medicine. Ed. S.H. Koslow, A.J. Mandell and F. Shlesinger. 1–15. N.Y.: Ann. NY Acad. Scis., 1987.]
- —. May, R.M. "Chaos and the Dynamics of Biological Populations." Nuclear Physics B. (Proc. Suppl.), 2 (1987), 225–246. [Reprinted in Chaos 87: International Conferences on the Physics of Chaos and Systems Far from Equilibrium. Ed. M. Duong—Van. 225–246. Amsterdam, 1987.]
- May, R.M. and M.P. Hassell. "Population Dynamics and Biological Control." *Phil. Trans. Roy. Soc. B.*, 318 (1988), 129–169. [Reprinted in *Biological Control of Pests, Pathogens and Weeds: Development and Prospects.* Ed. R.K.S.Wood and M.J. Way. 19–59. London: The Royal Society.]
- Anderson, R.M., R.M. May and A.R. McLean. "Possible Demographic Consequences of AIDS in Developing Countries." *Nature*, 332 (1988), 228–233.
- May. R.M. "Conservation and Disease." Consv. Biol., 2 (1988), 28-30.
- Anderson, R.M. and R.M. May. "Epidemiological Parameters of HIV Transmission." Nature, 333 (1988), 514–518.
- Hassell, M.P. and R.M. May. "Spatial Heterogeneity and the Dynamics of Parasitoid-Host Systems." Annales Zoologici Fennici, 25 (1988), 55–61.
- May, R.M. "How Many Species are There on Earth?" Science, 241 (1988), 1441–1449. [Reprinted in Biological Systems. Ed. B.R. Jasny and D.E. Koshland. 245–260. Washington, D.C.: AAAS, 1990.]
- May, R.M., R.M. Anderson and A.R. McLean. "Possible Demographic Consequences of HIV/AIDS Epidemics: I, Assuming HIV Infection Always Leads to AIDS." *Math. Biosc.*, 90 (1988), 475–505. [Reprinted in *Nonlinearity in Biology and Medicine*. Ed. A.S. Perelson, B. Goldstein, M. Dembo

and J.A. Jacquez. 475-505. N.Y.: Elsevier, 1988.]

- May, R.M. and R.M. Anderson. "The Transmission Dynamics of Human Immunodeficiency Virus (HIV)." Phil. Trans. Roy. Soc. B., 321 (1988), 565–607. [Reprinted in The Epidemiology and Ecology of Infectious Disease Agents. Ed. R.M. Anderson and J.M. Thresh. 239–281. London: The Royal Society, 1988.]
- Hassell, M.P., J. Latto and R.M. May. "Seeing the Wood for the Trees: Detecting Density Dependence from Existing Life-Table Studies." J. Anim. Ecol., 58 (1989), 883–892.
- May, R.M., R.M. Anderson and S.M. Blower. "The Epidemiology and Transmission Dynamics of HIV/AIDS." *Daedalus*, 118 (2) (1989), 163–201. [Reprinted in *Living with AIDS*. Ed. R.S. Graubard. 163–202. Cambridge, Mass.: MIT Press, 1989.]
- Anderson, R.M., R.M. May and S. Gupta. "Non-Linear Phenomena in Host-Parasite Interactions." *Parasitol*, 99 (1989), S59–S79.
- May, R.M. "The Chaotic Rhythms of Life." New Sci. (1989), 37–41. [Reprinted in Chaos. Ed. N. Hall. 82–95. London: Penguin, 1991.]
- Anderson, R.M., T.G. Ng, M.C. Boily and R.M. May. "The Influence of Different Sexual-Contact Patterns between Age Classes on the Predicted Demographic Impact of AIDS in Developing Countries." Ann. NY Acad. Scis., 569 (1989), 240–274.

[Reprinted in *Biomedical Science and the Third World: Under The Volcano*. Ed. B.R. Bloom and A. Cerami. 240–274. N.Y.: *NY Acad. of Scs.*, 1989.]

- Gupta, S., R.M. Anderson and R.M. May. "Networks of Sexual Contacts: Implications for the Pattern of Spread of HIV." AIDS, 3 (1989), 807–817.
- Pacala, S.W., M.P. Hassell and R.M. May. "Host-Parasitoid Associations in Patchy Environments." *Nature*, 344 (1990), 150–153.
- Sugihara, G. and R.M. May. "Applications of Fractals in Ecology." TREE, 5 (1990), 79-86.
- Anderson R.M. and R.M. May. "Modern Vaccines: Immunisation and Herd Immunity." Lancet, 335 (1990), 641–645. [Reprinted in Modern Vaccines. Ed. E.R. Moxon. 24–33. London: Edward Arnold, 1990.]
- Sugihara, G. and R.M. May. "Nonlinear Forecasting as a Way of Distinguishing Chaos from Measurement Error in Time Series." *Nature*, 344 (1990), 734–741.
- Hochberg, M.E., M.P. Hassell and R.M. May. "The Dynamics of Host-Parasitoid-Pathogen Interactions." Amer. Naturl., 135 (1990), 74–94.
- May, R.M. and R.M. Anderson. "Parasite-Host Coevolution." Parasitol., 100 (1990), S89-S101.

May, R.M. "How Many Species?" Phil. Trans. Roy. Soc. B., 330 (1990), 293-304.

- Sugihara, G., B. Grenfell and R.M. May. "Distinguishing Error from Chaos in Ecological Time Series." *Phil. Trans. Roy. Soc. B.*, 330 (1990), 235–251.
- Nowak, M.A., R.M. May and R.M. Anderson. "The Evolutionary Dynamics of HIV-1 Quasispecies and the Development of Immunodeficiency Disease." AIDS, 4 (1990), 1095–1103.
- Nee, S., P.H. Harvey and R.M. May. "Lifting the Veil on Abundance Patterns." Proc. Roy. Soc. B., 243 (1991), 161–163.
- Blower, S.M., D. Hartel, H. Dowlatabadi, R.M. Anderson and R.M. May. "Drugs, Sex and HIV: A Mathematical Model for N.Y. City." *Phil. Trans. Roy. Soc. B.*, 321 (1991), 171–187.
- Basson, M., J.R. Beddington, R.M. May. "An Assessment of the Maximum Sustainable Yield of Ivory from Elephant Populations." *Math. Biosc.*, 104 (1991), 73–95.
- Anderson, R.M., S. Gupta and R.M. May. "Potential of Community-Wide Chemotherapy or Immunotherapy to Control the Spread of HIV-1." *Nature*, 350 (1991), 356–359.

May, R.M. "Le Chaos en Biologie." La Recherche, 232 (1991), 588-599.

Pagel, M.D., R.M. May and A.R. Collie. "Ecological Aspects of the Geographical Distribution and Diversity of Mammalian Species." Amer. Naturl., 137 (1991), 791–815.

Nowak, M.A. and R.M. May. "Mathematical Biology of HIV Infections: Antigenic Variation and

Diversity Threshold." Math. Biosc., 106 (1991), 1-22.

Anderson, R.M., R.M. May, M.C. Boily, G.P. Garnett and J.T. Rowley. "The Spread of HIV-1 in Africa: Sexual Contact Patterns and the Predicted Demographic Impact of AIDS." *Nature*, 352 (1991), 581–589.

May, R.M. "El Caos en Biologia." Mundo Científico, 115 (1991), 746-754.

Hassell, M.P., R.M. May, S.W. Pacala and P.L. Chesson. "The Persistence of Host-Parasitoid Associations in Patchy Environments. I. A General Criterion." Amer. Naturl., 138 (1991), 568–583.

Nowak, M.A., R.M. Anderson, R.M. May, et al. "Antigenic Diversity Thresholds and the Development of AIDS." Science, 254 (1991), 963–969.

Hassell, M.P., H.N. Comins and R.M. May. "Spatial Structure and Chaos in Insect Population Dynamics." Nature, 353 (1991), 255–258.

Nee, S., R.D. Gregory and R.M. May. "Core and Satellite Species: Theory and Artifacts." OIKOS, 62 (1991), 83–87.

May, R.M. and G. Sugihara. "How Predictable is Chaos?" Nature (Sci. Corresp.), 355 (1992), 26.

Watts, C.H. and R.M. May. "The Influence of Concurrent Partnerships on the Dynamics of HIV/AIDS." Math. Biosc., 108 (1992), 89–104.

Nee, S. and R.M. May. "Dynamics of Metapopulations: Habitat Destruction and Competitive Coexistence." J. Anim. Ecol., 61 (1992), 37–40.

Gaston, K.J. and R.M. May. "Taxonomy of Taxonomists." Nature, 356 (1992), 281–282. [Reprinted in Italian: Sapere, No. 59, 14–16 (1993).]

May, R.M. "Concluding Discussion on the Meeting on Chaos." J. Roy. Stats. Soc. B., 54 (1992), 451–452.

-. "Density Dependent Populations." Nature (Sci. Corresp.), 356 (1992), 391-392.

Anderson, R.M. and R.M. May. "Understanding the AIDS Pandemic." Sci. Amer., 266 (1992), 58-66.

Anderson, R.M., R.M. May, T.W. Ng and J.T. Rowley. "Age-Dependent Choice of Sexual Partners and the Transmission Dynamics of HIV in Sub-Saharan Africa." *Phil. Trans. Roy. Soc. B.*, 336 (1992), 135–155.

May, R.M. "O Frágile Equilíbrio da Vida." Ciencia Hoje, 14 (1992), 18-25.

McLean, A.R. and R.M. May. "Understanding the Immune System: The Role of Mathematical Models." J. NIH Res., 4 (1992), 101–103.

Nowak, M.A. and R.M. May. "Coexistence and Competition in HIV Infections." J. Theor. Biol., 159 (1992), 329-342.

May, R.M. "How Many Species Inhabit the Earth?" Sci. Amer., 267 (1992), 42-48.

Comins, H.N., M.P. Hassell and R.M. May. "The Spatial Dynamics of Host-Parasitoid Systems." J. Anim. Ecol., 61 (1992), 735–748.

Nowak, M.A. and R.M. May. "Evolutionary Games and Spatial Chaos." *Nature*, 359 (1992), 826–829. May, R.M. "Marine Species Richness." *Nature* (Sci. Corresp.), 361 (1993), 598.

Nee, S. and R.M. May. "Population-Level Consequences of Conspecific Brood Parasitism in Birds and Insects." J. Theor. Biol., 161 (1993), 95–109.

Gupta, S., R.M. Anderson and R.M. May. "Mathematical Models and the Design of Public Health Policy: HIV and Antiviral Therapy." SIAM Review, 35 (1993), 1–16.

Agur, Z., Y.L. Danon, R.M. Anderson, L. Cojocaru and R.M. May. "Measles Immunization Strategies for an Epidemiologically Heterogeneous Population: The Israeli Study." Proc. R. Soc. B., 252 (1993), 81–84.

Nowak, M. and R.M. May. "AIDS Pathogenesis: Mathematical Models of HIV and SIV Infections." AIDS, 7 (Suppl 1: 92/93 Year in Review), (1993), S3–S18.

-... "The Spatial Dilemmas of Evolution." Intl. J. Bifurcation & Chaos, 3 (1993), 35-78.

Smith, F., R.M. May, R. Pellew, T.H. Johnson and K.S. Walter. "Estimating Extinction Rates." *Nature* (Sci. Corresp.), 364 (1993), 494–496.

- May, R.M. "Dinamiche Caotiche e Ritmi Biologici." Sfera, 36 (Special issue on "Caos e complessità"), (1993), 48–51.
- May R.M. and M.E.J. Woolhouse. "Biased Sex Ratios and Parasite Mating Probabilities." Parasitol., 107 (1993), 287–295.
- Smith, F., R.M. May, R. Pellew, T.H. Johnson and K.S. Walter. "How Much Do We Know about the Current Extinction Rate?" TREE, 8 (1993), 375–378.
- May, R.M. "Biological Diversity: Differences between Land and Sea." Phil. Trans. Roy. Soc. B., 343 (1994), 105–111.
- Nowak, M.A. and R.M. May. "Superinfection and the Evolution of Parasite Virulence." Proc. Roy. Soc. B., 55 (1994), 81–89.
- Smith, F.D.M., R.M. May and P.H. Harvey. "Geographical Ranges of Australian Mammals." J. Anim. Ecol., 63 (1994), 441–450.
- Nee, S. and R.M. May. "Habitat Destruction and the Dynamics of Metapopulations: Reply to Aldaz." J. Anim. Ecol., 63 (1994), 494.
- Heywood, V.H., G.M. Mace, R.M. May and S.N. Stuart. "Uncertainties in Extinction Rates." Nature (Sci. Corresp.), 368 (1994), 105.
- Nowak, M.A., S. Bonhoeffer and R.M. May. "More Spatial Games." Intn. J. Bifurcation & Chaos, 4 (1994), 33–56.
- Nee, S., E.C. Holmes, R.M. May and P.H. Harvey. "Extinction Rates Can be Estimated from Molecular Phylogenies." *Phil. Trans. Roy. Soc. B.*, 344 (1994), 77–82.
- S. Nee, R.M. May and P.H. Harvey. "The Reconstructed Evolutionary Process." Phil. Trans. Roy. Soc. B., 344 (1994), 305–311.
- Nowak, M.A., S. Bonhoeffer and R.M. May. "Spatial Games and the Maintenance of Cooperation." Proc. Natl. Acad. Sci., 91 (1994), 4877–4881.
- Hassell, M.P., H.N. Comins and R.M. May. "Species Coexistence and Self-Organizing Spatial Dynamics." *Nature*, 370 (1994), 290–292.
- May, R.M. "Conceptual Aspects of the Quantification of the Extent of Biological Diversity." *Phil. Trans. Roy. Soc. B.*, 345 (1994), 13–20. [Reprinted in *Biodiversity: Measurement and Estimation*. Ed. D.L. Hawksworth. 13–20. London: Chapman & Hall, 1995.]
- Lenski, R.E. and R.M. May. "The Evolution of Virulence in Parasites and Pathogens: Reconciliation between Two Competing Hypotheses." J. Theor. Biol., 169 (1994), 253–265.
- May, R.M. "Graeme Caughley and the Emerging Science of Conservation Biology." TREE, 9 (1994), 368–369.

--- "Ecological Science and the Management of Protected Areas." Biod. & Consv., 3 (1994), 437-448.

Tilman, D., R.M. May, C.L. Lehman and M.A. Nowak. "Habitat Destruction and the Extinction Debt." *Nature*, 371 (1994), 65–66.

- May, R.M. and M.A. Nowak, "Superinfection, Metapopulation Dynamics, and the Evolution of Diversity." J. Theor. Biol., 170 (1994), 95–114.
- Antia, R., B.R. Levin and R.M. May. "Within-Host Population Dynamics and the Evolution and Maintenance of Microparasite Virulence." Am. Nat., 144 (1994), 457–472.

Harvey, P.H., R.M. May and S. Nee. "Phylogenies without Fossils." Evolution, 48 (1994), 523-529.

- May, R.M. "Disease and the Abundance and Distribution of Bird Populations: A Summary." *Ibis*, 137 (1995), S85–S86.
- Nowak, M.A., R.M. May and K. Sigmund. "The Arithmetics of Mutual Help." Sci. Amer., 272 (1995), 76–81.
- Lipsitch, M., M.A. Nowak, D. Ebert and R.M. May. "The Population Dynamics of Vertically and Horizontally Transmitted Parasites." Proc. R. Soc. B., 260 (1995), 321–327.
- Nowak, M.A., R.M. May, R.E. Phillips, et al. "Antigenic Oscillations and Shifting Immunodominance in HIV-1 Infections." *Nature*, 375 (1995), 606–611.

- May, R.M. "Necessity and Chance: Deterministic Chaos in Ecology and Evolution." Bull. Amer. Math. Soc., 32 (1995), 291–308.
- Nowak, M.A., R.M. May and K. Sigmund. "Immune Responses against Multiple Epitopes." J. Theor. Biol., 175 (1995), 325–353.
- May, R.M. and M.A. Nowak. "Coinfection and the Evolution of Parasite Virulence." Proc. Roy. Soc. B., 261 (1995), 209–215.
- Hassell, M.P., O.Miramontes, R. Rohani and R.M. May. "Appropriate Formulations for Dispersal in Spatially Structured Models: Comments on Bascompte & Solé." J. Anim. Ecol., 64 (1995), 662–664.
- May, R.M. "Science and Everyday Life." Editorial in Science, 269 (1995), 1199.

Anderson, R.M., R.M. May and S. Gupta. "Genetic Heterogeneity in Helminths." Parasitol., 111 (1995), 537–538.

Bonhoeffer, S., A.V.M. Herz, M.C. Boerlijst, S. Nee, M.A. Nowak and R.M. May. "Explaining 'Linguistic Features' of Noncoding DNA." Science, 271 (1996), 14–15.

-... "No Signs of Hidden Language in Noncoding DNA." Phys. Rev. Letters, 76 (1996), 1977.

Nowak, M.A., S. Bonhoeffer and R.M. May. "Robustness of Cooperation." Nature, 379 (1996), 125-126.

Sheill, D. and R.M. May. "Mortality and Recruitment Rate Evaluations in Heterogeneous Tropical Forests." J. Ecol., 84 (1996), 91–100.

Gupta, S., M.C.J. Maiden, I.M. Feavers, S. Nee, R.M. May and R.M. Anderson. "The Maintenance of Strain Structure in Populations of Recombining Infectious Agents." *Nature Medicine*, 2 (1996), 437–442.

- Lloyd, A.L. and R.M. May. "Spatial Heterogeneity in Epidemic Models." J. Theor. Biol., 179 (1996), 1–11.
- Tilman, D. and R.M. May. "Species Fragmentation or Area Loss?" Nature (Sci Corresp.), 382 (1996), 215–216.
- Herz, A.V.M., S. Bonhoeffer, R.M. Anderson, R.M. May and M.A. Nowak. "Viral Dynamics In Vivo: Limitations on Estimates of Intracellular Delay and Virus Decay." Proc. Natl. Acad. Sci., 93 (1996), 7247–7251.

Rohani, P., R.M. May and M.P. Hassell. "Metapopulations and Equilibrium Stability: the Effects of Spatial Structure." J. Theor. Biol., 181 (1996), 97–109.

Nowak, M.A., R.M. Anderson, M.C. Boerlijst, S. Bonhoeffer and R.M. May. "HIV-1 Evolution and Disease Progression." Science, 274 (1996), 1008–1011.

Anderson, R.M. and R.M. May. "The Population Biology of the Interaction between HIV-1 and HIV-2: Coexistence or Competitive Exclusion?" AIDS, 10 (1996), 1663–1673.

Stone, L., G. Landau and R.M. May. "Detecting Time's Arrow: A Method for Identifying Nonlinearity and Deterministic Chaos in Time-Series Data." Proc. R. Soc. B., 263 (1996), 1509–1513.

Klenerman, P., R.E. Phillips, R.M. May, et al. "Cytotoxic T-Lymphocytes and Viral Turnover in HIV-1 Infection." Proc. Natl. Acad. Sci., USA, 93 (1996), 15323–15328.

May, R.M., D.J. Stekel and M.A. Nowak. "Antigenic Diversity Thresholds and Hazard Functions." Math. Biosci., 139 (1997), 59–68.

May, R.M. "The Scientific Wealth of Nations." Science, 275 (1997), 793-796.

Nowak, M.A., S. Bonhoeffer, G.M. Shaw and R.M. May. "Anti-Viral Drug Treatment: Dynamics of Resistance in Free Virus and Infected Cell Populations." J. Theor. Biol., 184 (1997), 203–217.

-. "Scientific Advance Thrives on Openness." Nature (Sci. Corres.), 389 (1997), 11.

-. "Science by the Country." Science (Letters), 276 (1997), 882-885.

Nee, S. and R.M. May. "Extinction and the Loss of Evolutionary History." Science, 278 (1997), 692-694.

Bonhoeffer, S., R.M. May, G.M Shaw and M.A. Nowak. "Virus Dynamics and Drug Therapy." PNAS,

94 (1997), 6971-6976.

May, R.M. "Kyoto and Beyond." Science (Editorial), 278 (1997), 1691.

- Nowak, M.A., D.C. Krakauer, A. Klug and R.M. May. "Prion Infection Dynamics." Integrative Biology, 1 (1998), 3–15.
- May, R.M. "The Scientific Investments of Nations." Science, 281 (1998), 49-51.
- -... "A Note of Climate Change." Cosmos, 8 (1998), 47-51.
- May, R.M. and S.C. Sarson. "Revealing the Hidden Costs of Research." Nature, 398 (1999), 457-459.
- Lloyd, A.L. and R.M. May. "Synchronicity, Chaos and Population Cycles: Spatial Coherence in an Uncertain World." TREE, 14 (1999), 417–418.
- May, R.M. "Science, Politics and Public Opinion: Tackling 'The Modern Dilemma:' The Wooldridge Lecture." *The Veterinary Record*, 145 (1999), 411–412.
- -. "Unanswered Questions in Ecology." Phil. Trans. R. Soc. Lond. B., 354 (1999), 1951-1959.

-. "Simple Rules with Complex Dynamics." Science, 287 (2000), 601-602.

- Wodarz, D., R.M. May and M.A. Nowak. "The Role of Antigen-Independent Persistence of Memory Cytotoxic T Lymphocytes." *International Immunology*, 12, No. 4 (2000), 467–477.
- Mace, G.M., May, R.M. and 13 others. "Duplicating Conservation Efforts." Nature (Sci. Corres.), 290 (2000), 714–715.
- —. "Relation between Diversity and Stability in the Real World." Science (Sci. Corres.), 290 (2000), 714–715.
- May, R.M. and M.P.H. Stumpf. "Species-Area Relations in Tropical Forests." Science, 290 (2000), 2084–2086.
- May, R.M. "Biotechnology: The Challenges." In J. Biolaw & Bus., Special Supplement (2000), 90-93.
- -. "Science and Society." Science, 292 (2001), 1021.
- -. "The Science of Climate Change." Science, 292 (2001), 261.
- Lloyd, A.L. and R.M. May. "How Viruses Spread among Computers and People." Science, 292 (2001), 1316–1317.
- May, R.M. "Risk and Uncertainty." Nature, 411 (2001), 891.
- May, R.M., S. Gupta and A.R. McLean. "Infectious Disease Dynamics: What Characterizes a Successful Invader?" Phil. Trans. R. Soc. Lond. B., 356 (2001), 901–910.

Profile

Dr. Norman Myers

Honorary Visiting Fellow, Green College, Oxford University

Education	and Academic and Professional Activities
1934	Born in August in the United Kingdom.
1958	B.A., Oxford University.
1958-1965	District Officer, Kenya Administration; High School Teacher in Kenya.
1963	Master's Degree, Oxford University.
1966-1969	Freelance writer, photographer and lecturer on African wildlife.
1970-1972	Attended the University of California, Berkeley.
1973	Ph.D., University of California, Berkeley.
1972—	Research projects for the U.S. National Academy of Sciences, the Royal Society
	in the United Kingdom, the Soviet Academy of Sciences, NASA, the World Bank,
	United Nations agencies, the OECD, WWF, and many other bodies.
	Honorary Visiting Fellow, Green College, Oxford University.
1983	Gold Medal, World Wildlife Fund.
1986	Gold Medal, New York Zoological Society.
1987	Special Achievement Award, Sierra Club.
1987	Distinguished Achievement Award, Society for Conservation Biology.
1989	Fellow, World Academy of Art and Sciences.
1992	Volvo Environment Prize.
1994	Member, U.S. National Academy of Sciences.
1995	Sasakawa Prize, United Nations Environment Programme.
1997	Appointed by Queen Elizabeth to the Order of St. Michael and St. George "For
	Services to the Global Environment."
2000	Ambassador, World Wide Fund for Nature/U.K.

To this day, Dr. Myers has pursued research independent of any single organization, being commissioned to conduct research into environmental problems on behalf of many international organizations while serving as a visiting professor at Harvard, Oxford and many other high-profile universities around the world. One of the characteristics of his research is his penchant for presenting and analyzing new topics ahead of the rest of the world.

Although the extinction of species was thought up to the 1970s to be proceeding at a rate of approximately one per year, Dr. Myers calculated that it was more likely occurring at a rate of one per day. In the late 1970s, he pointed out that the deforestation of tropical rainforests was proceeding at the tremendous rate of 75,000 square kilometers per year. These new suggestions were greeted with skepticism by many at first, but he was proved correct by the facts,

including analysis of satellite images.

In the late 1980s, he advocated the "hotspot" approach as the best way to conserve the species that were in the most trouble. This approach concentrates efforts on those areas with large concentrations of species facing extinction. This approach has been adopted by many environmental conservation organizations as a policy for conserving biodiversity.

Dr. Myers, who is well versed in both the natural and social sciences, has also led the world in analyzing such topics as environmental refugees and perverse subsidies. In addition to authoring several hundred scholarly articles, he continues to make a major contribution to progress toward a sustainable future for all through other publications and public appearances.

Essay

Our Environmental Future

Dr. Norman Myers

December 2001

The present generation stands at a vital turning point in human history. For the first time since we came out of our caves, entire segments of our planetary ecosystem face terminal threat through mass extinction of species, tropical deforestation, desertification, global warming and a host of other environmental problems. These are economic problems as well since our economies are ultimately dependent on the environmental resource base that supports all human activities. By safeguarding our environments, we are safeguarding our daily well-being too.

Shall we not say, then, that we are a privileged generation to live at a stage in the human enterprise when we have opportunity to save both our Earth and our world? If we succeed with this outsize challenge, we shall surely earn the thanks of numerous generations into the future. Indeed, we are a unique generation. No generation before us has ever faced a similar challenge, because the environmental problems have not remotely matched those of today. No generation that comes after us will ever face such a challenge, because if we do not overcome the problems, our descendants will have nothing left but to cope with the disaster that we pass on to them. It is up to us alone. Fortunately, we still have time to get on top of these problems before they get on top of us. Are we not fortunate beyond dreams to live at this unprecedented time?

Within this exceptionally creative context, a key question arises. What more can we do to surmount our environmental difficulties? In this essay, I propose that we give greater attention to two salient aspects of our challenge; two aspects that do not generally receive the attention they deserve. In fact, I consider they are the two most important factors in our environmental future. I shall plan to give priority attention to them through my research efforts in the coming years. This is research, moreover, that I could not undertake if it were not for the funding supplied by the financial generosity of the Blue Planet Prize.

1. The Future

We all spend a lot of the present thinking about the future. Business leaders focus on the next quarterly sales statement. Bankers fixate on the year-end returns on investment. Politicians are preoccupied with the next election. Citizens ponder all kinds of concerns, from next week to next year, to retirement time.

Whatever our situation and whatever our time horizon, we all "discount" the future. For each and every one of us, one dollar today is worth more than one dollar tomorrow. But consider: a sum of \$100 in fifty years discounted at an annual rate of 10% (a frequent rate as dic-

tated by capital markets) is worth less than \$1 today. Given the same discount rate of 10%, a cost of \$100 billion accruing in 100 years' time (through global warming for example) will have a present value of hardly more than \$7 million. With a more modest discount rate of 5%, a cost of \$1 billion in 100 years' time will have a present value of only \$87 million. Conversely, an investment of \$1 today (to counter global warming for instance) will, with a 5% discount rate, be worth almost \$18,000 in 200 years' time, and with a 10% discount rate it will be worth \$190 million.

The clincher factor is that a discount rate of 10% implies there is no future worth bothering about beyond seven years. Thus, the iron rule of the investment market.

Equally to the point, if the most valuable forest on Earth cannot make its "investment in the future" in less than seven years (most trees in the forest won't produce new adult trees in less than 10 years, more likely 20 years or more), it makes commercial sense for a logger to chop the whole lot down straight away and put the earnings into the stock market with its greater and quicker profit. It is financially rational, too, for a corporation to pursue activities with revenues of \$1 million this year even though it recognizes that in fifty years' time these activities will entrain environmental costs—such as writing off a potentially renewable resource—of \$100 million.

Thus arises the apparent shortsightedness of investors, if not their outright indifference to the future. It is not that they are truly shortsighted, rather they play by the rules of the marketplace as laid down by society. If society does not like the outcome, it is up to society to change the rules rather than shout foul at the investor (as is the inclination of certain environmentalists).

Within this framework, consider one particular environmental problem, the mass extinction that is overtaking the planet's species. This biotic crisis threatens not only to eliminate large numbers of species (conceivably tens of thousands per year already), but to reduce evolution's capacity to generate replacement species. This "end to birth" phase looks likely to endure for fully five million years and possibly several times longer. Just five-million years a period twenty times longer than humans have been humans—makes it impossible for us to postulate any realistic discount rate at all.

Moreover, the number of people affected within just five-million years could be as many as 500 trillion, or 10,000 times more people than have ever existed. (Just one trillion is a large number; figure out the length of time made up of one trillion seconds.) The "decision" on mass extinction being taken by the present generation—to allow it to proceed virtually unrestricted—will be far and away the biggest decision ever taken on the unconsulted behalf of future generations. In certain respects it will surely surpass all such past decisions combined. In this situation, are discount rates of any use at all?

This throws a new perspective on what is known as "intergenerational equity" or justice to future generations. The best books on this issue speak of no more than a dozen generations (300 years) ahead, beyond which the future is ostensibly unknowable and of scant practical interest anyway. While there is much uncertainty about what species are "good for," we are effectively saying we are completely certain that 200,000 future generations during those five million years will not be unduly disadvantaged through the mass extinction we are precipitat-

ing today. Yet our scientific understanding indicates the opposite is the case.

In any case, can we really envisage so many generations ahead? That is, can we identify with them, can we sense how they will cope with their future world, and imagine what will be their hopes and experiences? I must confess that I myself, for all my professional analysis of the future, cannot personally reach out in my mind beyond just a few generations. I hope one day to see some grandchildren, and I speculate on what sort of children they will eventually produce in turn. But five generations ahead is the best I can manage, try as I might. At the same time, I have to admit that my affluent lifestyle is surely serving to impose injury, however unintentionally, on the future world way beyond five generations, worth 125 years. Global warming, for instance, will degrade the planet for many hundreds of years.

Bottom line: we need a device in addition to discount rates to reflect our evaluations of the future. In fact, to reflect those evaluations that truly count. Relying on the supposed preferences of the marketplace means we would not bother in the least to safeguard the planet's forests, its oceans, its atmosphere or its ozone layer, let alone its climate. But because we do not have an economic alternative to conventional discounting, the case for forests, et cetera, tends to fail by default.

2. Environmental Surprises Ahead

Despite our inability to value the future in any way that makes sense in the long run, we should assume that the future will feature a host of surprises. Yet we suppose that surprises are an unusual, if not a rare, phenomenon. We should start to wrap our minds around the idea of a "surprise–rich" future, however, since surprises are likely to become ever more frequent within our lifetimes. They could also become the most significant single factor in the lives of businesspeople, politicians and, in fact, every single citizen.

Environmentalists view surprises in the technical sense of "discontinuities." A discontinuity arises when something suddenly happens to mark a profound change from the way things have been. For instance, when water cools, it eventually, and without warning, turns from a liquid to a solid, ice—all in a moment. It is the same when it heats and turns into a gas: steam. If you, the reader, are still puzzled, consider that we all have had first-hand experience of an absolute discontinuity, and one of a profoundly personal sort: when we were born. And a related discontinuity awaits us at the end.

We are acquainted with all kinds of other discontinuities. In the economic field, there's been the end of Japan's "bubble economy" in 1989, the abrupt emergence of OPEC, "Black Wednesday" on the U.S. Stock Exchange, and the recent upheavals in Asian financial markets. These crashes constantly take economists by surprise, as if crashes, however often repeated, lie entirely outside the established order of things. As is sometimes said, economists have predicted six of the last three recessions.

In terms of political discontinuities, recall the fall of the Berlin Wall and the end of South Africa's apartheid, plus the peaceful break-up of Czechoslovakia and the democratisation of the Philippines, South Korea, Argentina and Brazil. Also the peaceful collapse of the Suharto regime in Indonesia.

In the environmental arena, we should anticipate a host of discontinuities ahead. The

future certainly will not be a simple extension of the past in light of the expanding niche of humankind and its multifarious activities. It behooves come to us to grips with the idea of discontinuities so that they won't take us so much by surprise. Why do they ever take us by surprise? Well, because environmental problems are often problems of which we have scarcely thought.

These surprise phenomena deserve priority attention. Yet science has hardly touched on them. For the most part, they remain black holes of research. Among environmental discontinuities of the recent past—phenomena that should give us a clue about potential future events—are the "bleaching" of coral reefs with extensive morbidity and mortality throughout coral communities; mass mortality of dolphins and seals; phytoplankton blooms; cancer epizootics in marine turtles and fish; population declines among birds, especially North American and European migrants; and fast-growing die-offs of frogs among other amphibians in many parts of the world.

Still other environmental instances include the abrupt emergence of acid rain and the Antarctic ozone hole, likewise the collapse of the Peruvian anchovy fishery in the 1970s and the New England cod fishery in the early 1990s. Broadly viewed as environmental issues, too, are population surprises, notably the sudden soaring of population growth rates in one hundred countries during the 1960s, followed by steep plunges in a few countries in recent times. Who would have supposed that Iran, a fundamentalist Islamic state and as chauvinistic as they come, would need only 14 years to bring down its population growth rate from over 3%, to just 1% per year?

All these events have been unpredictable—or at least they have exceeded our present capacity to predict them. Entirely predictable is our readiness to be caught unawares time after time. We profess to have been surprised by the eruption of AIDS, yet the truly surprising thing is that we were surprised. It was surely inevitable that as huge numbers of people pressed deeper and deeper into tropical forests with their huge reservoirs of new pathogens, one would eventually make the leap from wild animals into humans, whereupon the pathogen would find itself in a bacterium's paradise, with human hosts travelling far and wide across landscapes local and global. As humans invade one "foreign" ecosystem after another, should we not anticipate a whole series of disease disasters?

All this raises a key question that should be at the top of any research agenda for environmentalists, also for economists and political analysts. What surprises should we anticipate for the foreseeable future. Hence, what can we do about them? What if China were to break up into half-a-dozen "Chinas," a not-impossible prospect? Think of the earthquake effects it would generate for global geopolitics. Or consider Saudi Arabia, only semi-stable at best with its lavish, untaxed and oil-subsidized lifestyles becoming unaffordable. What if its autocratic regime were to be undermined by educated princes returning from Harvard and Oxford universities, plus equally educated princesses told they must wear the veil, not drive a car and submit to numerous other restrictions? Were the Saudi regime to collapse or to be despatched by a coup, there would be a swift and sharp rise in oil prices, the spot market leaping to at least \$50 per barrel, conceivably \$75, not impossibly, \$100.

Still more seismic would be some environmental discontinuities, especially climate

changes. In the tropical Atlantic, water temperature can grow warmer and warmer without causing severe storms, but once it passes 28 degrees Celsius it starts to generate hurricanes. Even though the increase is merely incremental, it is enough to trigger a discontinuity of exceptional impact. What if, as is all too possible, Caribbean hurricanes no longer bypass Miami, but one of them were to land on top of the city? The damages could easily exceed \$100 billion, whereupon the discontinuity would immediately become economic as much as environmental.

Still more to the point, a globally warmed world could melt enough of the Greenland icecap to dislocate the currents of the North Atlantic. Result, the Gulf Stream could shift southwards and leave Britain turned into another Iceland. While this could not happen overnight, the prehistoric record shows it could occur in just a decade or two—lightning speed in terms of the economic traumas implied.

Given the many future global upheavals likely in a world with pressures from unprecedented growth in human numbers and human activities, we can surely expect that environmental changes will emerge faster, larger and more intense. In turn, these will entrain abundant discontinuities of both economic and political kinds, also social and cultural kinds, all arriving at once and making for super discontinuities. There could well be one discontinuity series after another, or rather side by side with each other, overtaking us at accelerating pace, and producing fundamental shifts in global systems of every sort from grand-scale ecosystems to nation states; in fact, the entire human enterprise.

Whether it will precipitate a shift in our understanding is debatable. Thus far, we have a scant idea of what discontinuities lie ahead, nor are we likely to know until they start to happen (if then). The expert in greatest demand will be the specialist in surprises. The secret is to spot those trends that are headed for terminal decline after long build-up of adverse forces bubbling away beneath the surface.

Reader, why not take a moment to try your hand at becoming such an expert—by looking beyond the headlines to seek out the true news. Attempt, in other words, a discontinuity in your own manner of thinking.

Lecture

Exploring The Frontiers of Environmental Science

Dr. Norman Myers

I am deeply grateful to the Asahi Glass Foundation for awarding me this prestigious prize. There are two particular reasons why I feel so appreciative. First, I pursue environmental science in a way different from most of my colleagues around the world. I work on my own as an independent scientist, which is a form of career not usually recognized by a major award. Secondly, you have selected me for work that spans a range of environmental fields: biodiversity, evolution, forests, eco-agriculture, environmental security, population, resource economics and sustainable development. My research is interdisciplinary, spanning both the life sciences and the social sciences. The environmental challenge covers a host of factors with multiple interactions and as such it requires interdisciplinary science. In fact, I specialize in being a generalist, which, like my independent status, is different from what most scientists do—and hence it too is rarely recognized through a top-rank prize. Your award will send a strong message to start-out environmental scientists that they may well be applauded if they pursue an independent or an interdisciplinary career, preferably both.

Let me illustrate with some examples of my environmental research—examples that also illustrate how I have attempted to explore some frontiers of environmental science. In this latter respect too, I sometimes depart from mainstream science. Whereas many scientists concentrate on supplying new answers to established questions, I also prefer to ask if we are raising all the right questions in the first place.

1. Mass Extinction of Species

In 1971, I started to demonstrate that we are into the opening phase of a mass extinction of species. Far from accepting the conventional estimate that species were disappearing at a rate of one per year—a view long established among scientists, conservationists and governments—I calculated that the extinction rate was at least one species per day, possibly many times more. At first my findings were dismissed as exaggerated, but they were eventually proved correct by other scientists' analyses. I have subsequently refined my assessment several times, always with the same conclusion: that we are starting to witness the greatest depletion of life's abundance and variety since the demise of the dinosaurs and associated species 65-million years ago. There is much evidence, albeit less than conclusive, that we could already be losing tens of thousands of species every year, and at a rate at least one-thousand times greater than the "background" rate of the prehistoric past.

2. Tropical Deforestation

In 1978, I undertook a U.S. National Academy of Sciences project to investigate the true rate of tropical deforestation. Using remote sensing data, I demonstrated that the rate was at

least 2.5 times greater than had been conventionally supposed, and a rate that was accelerating rapidly. Since tropical forests contain the majority of Earth's species and were being depleted faster than any other ecological zone, I identified the forests as the main locus of the mass extinction underway. While my deforestation findings were viewed in some quarters as alarmist, they were subsequently confirmed by other scientists' surveys. I convened a United Nations conference to get the issue established on political agendas. In 1989, I undertook a follow-up assessment that supported my earlier projections of deforestation.

3. The Hamburger Connection

Also on the deforestation front, I started in the early 1980s to show that the overall problem was not limited to tropical forest countries. It could also originate in developed countries through, for example, their marketplace demand for artificially cheap beef as epitomized through "the hamburger connection" between North America and Central America, and "the cassava connection" between Europe and Southeast Asia. In the first instance, the beef was raised on forestlands converted into pasture, and in the second instance, the cassava, being a rich livestock feed for cattle in Europe, was grown on plantations established by clearing tropical forests. This time I ran into trouble from a hamburger corporation that threatened me with a lawsuit for damages totalling \$3 million.

I subsequently documented North/South linkages of similar sort with respect to desertification in the Sahel through European governments' support of export crops, such as groundnuts and cotton, and with respect to desertification in Southern Africa by virtue of beef subsidies from the European Community. The upshot in all these cases was that environmental degradation was caused by marketplace demand from countries way beyond the horizon from where the degradation occurred. It was a case of looking beyond **symptoms** of problems to **sources** of problems—a more productive way to tackle environmental challenges in their full scope.

4. The Triage Concept for Threatened Species

Also in the early 1980s, I broached the concept of "triage" with respect to threatened species. The concept postulates that since we have far too few conservation resources to assist all species under threat, we are obliged to choose (whether deliberately or not) between species: some warrant our support, others cannot. While the choice is rarely made in systematic fashion, it is effectively and increasingly made as an in-built determinant of our save-species efforts. Hence there is a premium on making conservation decisions by design rather than by default. Americans have assigned \$15 million to saving a single species, the California condor, whereas the same sum could go far to preserve 200 threatened mollusc species in the Mississippi River system—yet the implicit trade-off has hardly been addressed.

I devised a series of evaluatory criteria by which we can make selective judgements for and against particular species, and do it in informed and methodical fashion. These criteria were based on biological, ecological, genetic, evolutionary, economic, aesthetic and ethical factors. My analyses were eventually adopted as an operational principle by a number of conservation organizations. Much the same analysis applies of course to entire ecosystems and even biomes. Should we not be making a super priority of tropical forests (even if that is to the detriment of other biomes) on the grounds that the forests feature the great majority of extinctions both present and prospective? These are very hard decisions, demanding the best scientific insights we can mobilize.

5. Tropical Forests and Climate

In the mid-1980s, I synthesized data from the main sectors of the humid tropics to show that contrary to much conventional thinking, tropical forests can indeed influence climate, whether at local, national, regional or even global levels. The forests manifest their influence through disruption of rainfall regimes, increase in the albedo effect, and buildup of greenhouse gases in the atmosphere. More importantly, I evaluated the biomass dynamics of tropical forests with respect to their carbon sinks, concluding that despite established thinking (again), tropical forests play a pivotal role in the global carbon budget insofar as they contain fully one-fifth of all carbon held in the planet's plants and soils. When the forests are burned, they release their carbon, contributing very roughly one-quarter of carbon dioxide build-up in the global atmosphere. I subsequently developed these findings via the Intergovernmental Panel on Climate Change into a mode to mitigate global warming through enhanced forest conservation and reforestation.

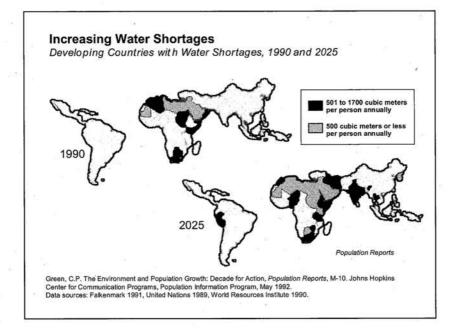
6. Economic Value of Species and Genetic Resources

Also in the mid-1980s, I returned to species, assessing the economic values of their genetic resources and with particular respect to sectors such as medicine, agriculture, industry and energy. I calculated that, for instance, the two anti-cancer drugs from the rosy periwinkle generated commercial sales of \$200 million per year worldwide, while economic values in terms of the 70,000 working lives saved each year were worth several times more. I further estimated that the commercial value of all plant-derived pharmaceuticals was at least \$40 billion per year, yet we enjoyed their benefits after scientists had conducted intensive assessment of only one plant species in one hundred.

This was the first occasion of demonstrating the capacity of species to exert their financial strength in the marketplace. The findings proved offensive to certain colleagues, some of whom protested that my research was "evil" on the grounds that any species, being unique, is beyond value by definition. Fortunately, the analytic methodology was accepted by the World Health Organization.

7. Environmental Security

Also in the mid-1980s, I broached an entirely new field: the environmental dimension to security issues. I was struck by the Gorbachev warning that the threat from the skies was not so much nuclear missiles but ozone-layer depletion and global warming. I had heard from Middle East leaders that a basic source of the Israel/Arab conflict was not oil but another liquid, water. There were many other potential water conflicts, for instance between Egypt and Ethiopia over the River Nile. By 2025, there could be three-billion people suffering water shortages, the bulk of them sharing international river basins.

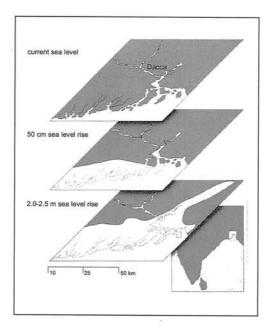


There are still further illustrations of environmental security, notably desertification, deforestation and fuelwood shortages, all with scope for civil strife, outright violence and military confrontation. I persuaded the World Commission on Environment and Development, a member of which was the Japanese Foreign Minister Mr. Saburo Okita, that its report should include a chapter on these new threats to security. I produced follow-up analyses on population and conflict, examining population pressures as a cause of violence in Rwanda, for example. The overall rationale has been adopted as the underpinnings of security appraisals by nations such as the United States, the United Kingdom, Norway, India and Australia. In 1997, I briefed a conference at the Pentagon in Washington, D.C., attended not only by military experts but by leaders from the White House, the U.S. State Department and the National Security Council. As a result of this conference, there is now a Pentagon department dealing with environmental security.

8. Environmental Refugees

As a subset of Environmental Security, I have investigated the emergent problem of environmental refugees. These are people who feel driven from their homelands for environmental reasons such as soil erosion, water shortages, desertification and fuelwood deficits, plus associated factors, such as population pressures. In the mid-1990s, I calculated that these refugees numbered 25 million, a total greater than all other forms of refugees put together. Their number may well double by 2010, and even reach 200 million in a global warmed world. This is an entirely new phenomenon, with major policy implications for the global community.

PEOPLE AT RISK IN A GLOBALLY-WARMED WORLD				
Country/Region	Millions at risk			
China	77			
Bangladesh	28			
India	23			
Egypt	15			
Island States	1			
Drought areas	60			
Total	204			

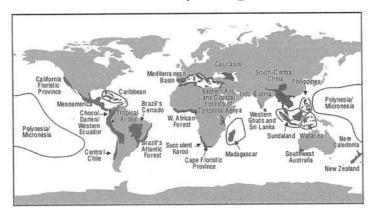


9. Biodiversity Hotspots

In the late 1980s, I returned to species questions. I developed the concept of "biodiversity hotspots," these being areas that feature exceptional concentrations of endemic species in habitats subject to exceptional threat of destruction. Through follow-up analyses in conjunction with Conservation International in Washington, D.C., I have found that over two-fifth of Earth's plant species and over one-third of vertebrate species (except fish) are confined to 25 localities that make up just 1.4 percent of Earth's land surface, these being localities where the species face severe threat of extinction. The 25 hotspots are so environmentally degraded that they have lost at least 70 percent, often 90 percent, of their original vegetation, and look likely, in the absence of expanded conservation efforts, to lose much of the rest within a few decades.

The hotspots analysis has pointed the way to "silver bullet" responses on the part of conservation planners. This contrasts with the scattergun approach of traditional practice that has often sought to be many things to many threatened species, and through insufficient funds has ended up by failing to be much to most such species. The hotspots strategy has been adopted by the World Bank, the Global Environment Facility, the MacArthur Foundation, Conservation International, and several other front-rank organizations in the conservation arena.

Biodiversity Hotspots



Because of the cost-effective nature of the hotspots strategy, the amount invested in hotspots has topped \$600 million in 10 years, the largest sum ever assigned to a single conservation strategy. All 25 hotspots could be safeguarded for only \$500 million per year, a tiny fraction of what governments, international agencies and citizen groups currently spend on conservation. The sum of \$500 million is only twice as much as the Pathfinder mission to Mars, justified largely on biodiversity grounds, vis-à-vis the search for extraterrestrial life. To put it in further perspective, the sum is equivalent to one-twentieth of what Europeans spend on ice cream each year. Were we to preserve the 25 hotspots, we would likely reduce the mass extinction by at least one-third. No other strategy available could accomplish so much for so little.

10. Future Evolution

I have also examined the future course of evolution. In the early 1980s, I began to raise questions about what the current biotic crisis would do to basic evolutionary processes, such as speciation, origination and adaptive radiation. I concluded that the crisis would not only eliminate large numbers of species, but, still more significantly, it would deplete the capacity of evolution to generate replacement species within a recovery phase of 5-10 million years (the usual period following the five mass extinctions of the prehistoric past). The crisis would have this depletive effect by degrading, if not destroying, tropical forests and wetlands that in the prehistoric past have served as the main "powerhouses" of evolution, supplying the bulk of replacement species following mass extinctions. That is to say, the present crisis would severely curtail evolution's capacity to make good the losses of the current mass extinction: "Death is one thing, an end to birth is something else."

In short, we look set to impoverish the planet for a period at least twenty times longer than humans have been humans. The number of future people affected could, in principle, be as many as 10,000 times more than have existed to date. The implicit "decision" we are taking today—through our lack of sufficient action and through its impact on the unconsulted behalf

of future generations—is surely the biggest decision in the whole of human history, yet it is almost entirely disregarded by the public and its political leaders. It was tackled for the first time by the scientific community through an international conference that I organized in 1999 through the U.S. National Academy of Sciences.

11. Perverse Subsidies

In the late 1990s, I took a further look at some sources of environmental problems, as opposed to the symptoms of problems that often attract more attention. I analysed those subsidies that exert adverse impact on, not only our environments, but our economies as well. Leading categories include agriculture, fossil fuels, road transportation, water, forests and fisheries. These "perverse" subsides amount to around \$2 trillion a year worldwide, hence they have marked capacity to distort our economies in addition to inflicting grandscale injuries on our environments. On both counts, they foster unsustainable development. Ironically the total of \$2 trillion is 3.5 times higher than the Rio Earth Summit's budget for sustainable development—a sum that governments dismissed as quite unavailable.

Perverse subsidies are those whic to both the environment and th	
Over-productive agriculture	510
Fossil fuels/nuclear energy	300
Road transportation	780
Mis-use and over-use of water	230
Over-harvesting of fisheries	25
Over-logging of forests	92
Total	1,950
By definition, these are funds going to support un Contrast the Rio Earth Summit budget for sus \$600 billion per year.	

Were the perverse subsidies to be phased out, there would be a double dividend. Firstly, the savings would enable governments to revise their fiscal priorities by, for example, cancelling their budget deficits at a stroke and markedly increasing their health and education outlays. Secondly, there would be an end to government support (unwitting as it is) for environmental degradation. In fact, reduction of perverse subsidies would do more for both our environments and our economies than any other single measure.

There are sizeable political obstacles to cancelling the subsidies. In Washington, D.C., the Congress is subject to special interests' lobbying to the extent of \$100 million a month. Fortunately, a number of countries have demonstrated that the political obstacles can be overcome. New Zealand, a nation more dependent on agriculture than any other developed nation, has got rid of virtually all its agri-subsidies. Several other nations have slashed their subsidies in the other four sectors. Meantime, a typical American taxpayer funds the subsidies with \$2,000 per year, then pays out another \$1,000 through environmental repair costs.

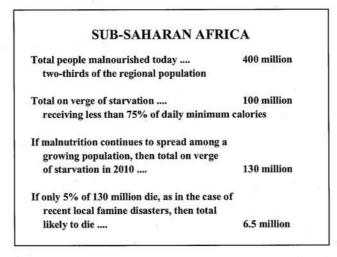
12. Sustainable Agriculture

I have examined the challenge of increasing food output by half within the coming two decades, plus the associated challenge of doing it through sustainable agriculture. Of course this is not a new issue, very much the contrary. But many experts assert that conventional agriculture is ever-more successful as witness declining grain prices. Unfortunately, they do not build into their calculus the parallel decline of the environmental resources underpinning long-term agriculture, notably through soil erosion, water deficits, and pollution of several sorts, let alone climate change.

I assessed the depletive impact of the over-loaded resource base through policy appraisals for the World Food Summit in 1996. I showed that if these environmental problems were to be factored in, grain prices would surely be soaring and thus sending urgent messages for adoption of sustainable agriculture via an Evergreen Revolution.

13. Food and Hunger in Sub-Saharan Africa

Following my 24 years of living in Sub-Saharan Africa, I have recently assessed the food prospects for the region. Since 1960, and as per-capita food production has declined, many people have become steadily hungrier. I have calculated that two out of three people are now malnourished, twice as many as officially estimated. Yet governments and development agencies seem largely indifferent to the adverse trend; their implicit response, by virtue of their lack of sufficient action, is to suppose it can be allowed to keep on declining indefinitely. Of course this is the opposite of what they intend, but their record implies as much.



I have demonstrated that the downward spiral cannot long continue before people cease to grow more hungry. They will start to die, and in unprecedently large numbers. (This is not to ignore that in certain countries the overwhelming source of mortality will lie with AIDS a disease that is potentiated by malnutrition, and vice versa.) Fortunately, there are vigorous and urgent initiatives available to raise food output and to slow population growth, both possible as witness the efforts of a few enlightened countries, whereupon the region could become self-sufficient in food within two decades.

14. New Consumers

Seventeen developing and three transition nations now feature over one-billion people with enough household income to enjoy meat every day and to buy cars in fast-growing numbers. Already they possess purchasing power matching that of the United States. Their numbers may well increase by half by 2010, and their purchasing power by still more. Their strongly meat-based diet entails environmental problems in that the meat is often raised on grain, which overloads croplands and diverts much water in countries with water shortages. The new consumers possess 125-million cars or 22 percent of the global fleet, and by 2010 the total could jump to 300-million cars or 38 percent. Cars not only cause much local pollution, but are the fastest growing source of carbon dioxide emissions, which contribute roughly half of global warming processes.

NEW CONSUMERS	NEW CONSUMERS' CARS (millions)		
Total new consumers today:		Total 1999	Projected 2010
1.07 billion (300 million in China, 140 million in India)	20 New Consume countries	r 125	230
	United States	162	185
and with collective purchasing power of PPP\$6.1 trillion,	World	525	800
almost equivalent to the United States	Cars are the faste	est-growing source	of CO2 emissions— nissions worldwide.

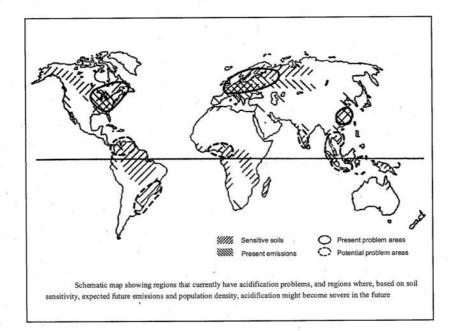
Of course, these people should be enabled to enjoy their new found affluence, provided they do not impose undue environmental and hence economic harm at both local and international levels. Hopefully, the new consumers can learn from the mistakes, also the positive experiences, of the long affluent nations in order that their environmental impacts remain acceptable. Hopefully too, the rich-world consumers can be persuaded to adopt less environmentally harmful lifestyles, which could then serve as models for the new consumers. There is much scope for "Factor Four" and even "Factor Ten" reductions in energy use, greater recycling of materials, enhanced pollution controls and other forms of waste management, in fact, resource conservation all round.

15. Environmental Surprises

I suspect that my main scientific contribution may eventually prove to be my research into environmental problems that hitherto remain unknown, or at least unrecognized. At the 1972 Stockholm Conference on the Human Environment, there was no mention of what have subsequently come to be acknowledged as front-rank problems: mass extinction of species, tropical deforestation, desertification, ozone-layer depletion, and climate change. With 20/20 hindsight (that exact science), we can now see that with greater inclination to raise new questions, scientists could have identified some of these problems ahead of time, and thus moved to forestall them. I believe that the biggest environmental problems ahead could well be ones we have not even thought of as yet—but that we could pinpoint with a more expansive approach to research agendas.

Many "environmental surprises" are likely to arise in the form of what are technically known as discontinuities, or non-linear switches in patterns and processes, often brought about by synergized interactions between two or more environmental problems. The stock example of a discontinuity lies with water, which can suddenly turn from a liquid into either a solid or a gas. Environmental discontinuities have included deforestation-derived declines in tropical rainfall, ozone-layer depletion and global warming. In the biodiversity field, there have been abrupt mass mortalities of dolphins and seals, phytoplankton blooms, cancer epizootics in fish, bleaching of coral reefs, and the precipitous decline of Peru's anchoveta fishery and amphibians worldwide. We have also witnessed many synergized interactions, such as acid rain and wild fires in conjunction with over-heavy logging of tropical forests.

Both discontinuities and synergisms are recognized by scientists to be among the most important phenomena in nature, and they are likely to become more frequent in a world of increasing environmental pressures among other problems (economic, social, political). Yet they receive only a fraction of the research attention they deserve, despite ground-breaking research such as my colleague Professor May has cited with respect to chaos theory and related issues. I plan to use part of the Blue Planet funds to press ahead with research on the issue from the standpoint of intersectoral linkages with their many policy implications. Fortunately, there can be positive discontinuities in the policy arena, generating reinforced leverage and multiplier effects, as witness the Ozone Layer Treaty, the plunge in birth rates in several countries, and the start on slashing perverse subsidies.



These 15 issues are what I regard as my main research products. They began in the early 1970s when I was still a student at the University of California and I raised the warning about the mass extinction of species underway. That was also the time of the Stockholm Conference on the Human Environment, and as noted above, I was struck that the participants made no mention of mass extinction as a major environmental problem. Nobody had thought to ask if it was a problem at all, even though if it had been recognized we could have done more to reduce its ultimate scope.

Nor did the scientists at Stockholm mention any of several other issues (listed above) that subsequently came to be recognized as front-rank environmental problems. All of them could, with a modicum of readiness to look beyond conventional thinking, have been brought to the urgent attention of political leaders. It was this that persuaded me that the best scientific career I could follow would be, not so much to generate new answers to recognized questions, but to ask if we are raising all the right questions in the first place. It is an unusual form of career—and in retrospect the most stimulating I could have chosen. What a rewarding life it has been: wandering around on the horizons of environmental science, seeking one new question after another—and doing it at a time when environmental science is needed in its full scope if it is to support our Earth and our world.

Conclusion

In summary, there have been three dimensions to my professional career. I have worked as independent scientist. I have practised interdisciplinary science. I have preferred to identify new questions. None of these fits the usual mould of science. This returns me to the main reason why I am specially pleased to be selected for your Blue Planet Prize. You have recognized a scientist who has long stood apart from mainstream science. I hope this helps you to understand how much I welcome your gesture. Moreover, through your award you have set me free financially to tackle those environmental questions that I consider most important. I can now set out on what I hope will be the most productive phase of my entire career.

I also like to think you have selected me not just as an environmental scientist but as an environmental activist. Right from my start in 1970, I have made it a rule to take my research findings and policy recommendations to governments, international agencies and political leaders in dozens of countries. I have pressed the environmental cause with prime ministers and presidents on four continents, with the head of the World Bank and United Nations agencies, and with corporate chiefs in many lands, including Japan. In addition, I have publicized the environment on television and radio and through newspapers and magazines. I have addressed 5,000 people in London and I have sat down in front of bulldozers in Australia. I hope that, through your selection of me for your Prize, you are encouraging more scientists to jump into the public arena and alert the world to our environmental problems—and our opportunities. These voices are sorely needed.

A Concluding Comment. We live at an altogether unprecedented time in human history. Entire segments of our planetary ecosystem face terminal threat through deforestation, desertification, global warming and a host of other environmental problems. This prompts an overriding thought. Are we not a privileged generation to live at a time when we have opportunity to save both our Earth and our world? No generation in the past has enjoyed such an opportunity, since the problems were not there. No generation in the future will enjoy the same opportunity, because if we do not get on top of the problems before they get on top of us, our descendants will have nothing left to do but to pick up the pieces we pass on to them. We are fortunate indeed to live at a time of such a once-and-for-all challenge. It is a super-size challenge, and if we measure up to it, we shall surely feel five metres tall. Above all, we shall earn the thanks of numerous generations to come.

Major Publications

Dr. Norman Myers

Books

- Myers, N. The Long African Day. N.Y. and London: MacMillan, 1972. (Three printings).
- —. Conversion of Tropical Moist Forests (Report to National Academy of Sciences). Washington, D.C.: National Research Council, 1980.
- —. A Wealth of Wild Species. Boulder, Colorado: Westview Press, 1983. (Four book clubs and two science awards).
- -... The Primary Source: Tropical Forests and Our Future. N.Y. and London: Norton, 1984. (Second edition, 1985. Third enlarged edition, 1992).
- --. The Gaia Atlas of Planet Management. London: Doubleday, and N.Y.: Pan Books, 1984. (Twelve translations. Fully revised and expanded edition, 1993.)
- Myers, N., D.O. Hall and N.S. Margaris, ed. *Economics of Ecosystem Management*. Dordrecht: W. Junk Publishers, 1985.
- Myers, N. The Gaia Atlas of Future Worlds: Challenge and Opportunity in an Age of Change. N.Y.: Doubleday, and London: Robertson McCarta, 1990.
- ---. Population, Resources and the Environment: The Critical Challenges. N.Y.: United Nations Population Fund, 1991. (French and Spanish translations).
- Myers, N., ed. Tropical Forests and Climate. Dordrecht: Kluwer Academic Publishers, 1992.
- —. The Environmental Basis of Political Stability. N.Y.: Norton, and Washington, D.C.: Island Press, 1993; Ultimate Security, 1996. (Chinese translation. Shanghai: Shanghai Publishing House, 2001.)
- Myers, N. and Julian Simon. *Scarcity or Abundance: A Debate on the Environment*. N.Y.: Norton, 1994. (Italian translation, 1995).
- Myers, N. and J. Kent. *Environmental Exodus: An Emergent Crisis in the Global Arena*. Washington, D.C.: The Climate Institute, 1995. (Italian translation, 1999).
- -... Perverse Subsidies. Winnipeg, Canada: International Institute for Sustainable Development, 1998.
- Myers, N., R.A. Mittermeier, P.R. Gil and C.G. Mittermeier. *Biodiversity Hotspots*. Monterrey, Mexico: CEMEX Publishers, 1999. (Distributed outside Mexico by Univ. of Chicago Press).
- Myers, N. Towards a New Greenprint for Business and Society. Tokyo, Japan: Tachibana Publishing, 1999. (In Japanese. Korean translation, 2000).
- Myers, N. and J. Kent. *Perverse Subsidies: How Tax Dollars Can Undercut the Environment and the Economy*. Washington, D.C.: Island Press, 2001.
- -... One Billion New Consumers: The Influence of Affluence. 2002. (In prep.)

Refereed publications

Myers, N. "Wildlife and Development in Uganda." Bioscience, 21 (1971), 1071-5.

- -. "National Parks in Savannah Africa." Science, 173 (1972), 1255-63.
- -... "A Preliminary Appraisal of the Ecological and Socioeconomic Consequences of a Proposed Tourist Development of Kenya's South Coast." Report to World Bank, Nairobi, Kenya. 1972.
- —. "The Masai: Modernizing the Myth." Association of Pacific Coast Geographers Yearbook, 35 (1973), 147–164.
- -... "The Spotted Cats: In Danger-or in Danger of Danger?" In *The World's Cats, Ecology and Conservation*. Vol. I. Ed. R.L. Eaton. 276-320. Winston, Oregon: World Wildlife Safari, 1973.
- —. "Status of the Leopard and Cheetah in Africa and of the Jaguar and Ocelot in the Amazon." In Cats of the World. Ed. N. Sitwell. 16–27. London: Tom Stacey, 1973.

- -. "National Parks and Land-Use Planning." Ekistics, 36/214 (1973), 223-229.
- -. "Leopard and Cheetah in Ethiopia." Oryx, 12 (2) (1973), 197-205.
- —. "The Ecologic-Socioeconomic Interface of Wildlife Conservation in Emergent Africa: Lakes Nakuru and Naivasha in Kenya." J. Environmental Economics and Management, 1 (1974), 319–334.
- —. "Institutional Inputs for Cheetah Conservation in Africa." Transactions of 39th North American Wildlife and Natural Resources Conference, 1974, 323–328.
- -. "The Whaling Controversy." American Scientist, 63 (4) (1975), 448-455.
- —. "The Tourist as an Agent for Development and Wildlife Conservation: The Case of Kenya." Intl. J. Social Economics, 2 (1) (1975), 26–42.
- —. "The Cheetah Acinonyx Jubatus in Africa." IUCN Monograph No. 4. Morges, Switzerland: IUCN, 1975.
- -. "An Expanded Approach to the Problem of Disappearing Species." Science, 193 (1976), 198-202.
- --. "China's Approach to Environmental Conservation." Environmental Affairs, 5 (1) (1976), 33-63.
- —. "The Leopard Panthera Pardus in Africa." IUCN Monograph No. 5. Morges, Switzerland: IUCN, 1976.
- -. "The Cheetah in Africa under Threat." Environmental Affairs, 5 (4) (1977), 617-647.
- —. "The Cheetah's Relationships to the Spotted Hyena: Some Implications for a Threatened Species." In Proceedings of the 1975 Predator Symposium (American Society of Mammalogists). Ed. R.H. Phillips and C. Jonkel. (1977) 191–200.
- -... "Discounting and Depletion: The Case of Tropical Moist Forests." Futures, 9 (6) (1977), 502-509.
- —. "Wildlife of Savannah and Grasslands: A Common Heritage of the Global Community." In Proceedings of Earthcare Conference. Ed. E. Schofield. 385–409. Boulder, Colorado: Westview Press, 1978.
- -. "What Use is Wildlife?" Earthscan Briefing Document 11. London: Earthscan, 1978.
- —. "The Global Problem of Tropical Deforestation." Keynote paper in Proceedings of U.S. Strategy Conference on Tropical Deforestation. 19–22. Washington, D.C.: Department of State, 1978.
- -. "Institutional Inputs for Conservation of the World's Cats." The World's Cats, 3 (1978), 74-76.
- —. "The Sinking Ark." Oxford and N.Y.: Pergamon Press, 1979. (Third printing, 1983. Translations in four languages.)
- —. "Tropical Biomass Systems." In Future Sources of Organic Raw Materials. Ed. L.E. St.-Pierre and G.R. Brown. 343–354. N.Y.: Pergamon Press, 1980.
- --- "Bio-Energy for Kenya: Some Technical Possibilities." In Energy and Environment in East Africa.
- 250–258. Nairobi, Kenya: United Nations Environment Programme, 1980.
- —. "Present Status and Future Prospects of Tropical Moist Forests." Environmental Conservation, 7/2 (1980), 101–114.
- -. "Playing God to Save Diversity." Technology Review, 82/5 (1980), 62-63.
- —. "Multinational Timber Corporations and Tropical Forests." N.Y.: Council for Economic Priorities, 1980.
- -... "Bailing Out the Ark." Bioscience, 30/8 (1980), 553-556.
- -. "What Future for Amazonia?" Americas, 32/10 (1980), 18-25.
- -. "The Problem of Disappearing Species: What Can Be Done?" Ambio, 9/5 (1980), 229-235.
- —. "Conversion of Tropical Moist Forests" (Report to National Academy of Sciences). Washington, D.C.: National Research Council, 1980.
- -. "The Exhausted Earth." Foreign Policy, 42 (1981), 141-155.
- -... "The Hamburger Connection: How Central America's Forests Become North America's Hamburgers." Ambio, 10/1 (1981), 3-8.
- —. "Conservation Needs and Opportunities in Tropical Moist Forests." In *The Biological Aspects of Rare Plant Conservation*. Ed. H. Synge. 141–154. Chichester, U.K.: John Wiley, 1981.

- -. "Corn Genes and Big Dollars." Technology Review, 84/2 (1981), 8-9, 64.
- —. "Conserving Marine Genetic Resources in Protected Areas." In Conserving the Natural Heritage of Latin America and the Caribbean. 42–51. Gland, Switzerland: IUCN, 1981.
- —. "The Leopard in Africa: Biological and Cultural Realities." Intl. J. for Study of Animal Problems, 2/1 (1981), 5–6.
- -. "Corporate Destruction of Tropical Forests." Business and Society Review, 39 (1981), 9-13.
- —. "Tropical Forests as Sources of Pharmaceuticals and Industrial Products." Tropical Silviculture. International Union of Forest Research Organizations, 4 (1981), 1–6.
- —. "Non-Market Values of Tropical Forests: Species." In *Benchmark Papers in Tropical Ecology*. Ed. C.F. Jordan. N.Y.: Academic Press, 1981.
- —. "Deforestation in the Tropics: Who Gains, Who Loses?" Studies In Third World Societies, 13 (1982), 1–24.
- —. "Conversion Rates in Tropical Moist Forests." In *Tropical Rain Forest Ecosystems*. Ed. F.B. Golley, H. Lieth and M.J.A. Werger. 289–300. Amsterdam, Netherlands: Elsevier Publishing, 1982.
- —. "Conservation of Rain Forests for Scientific Research, for Wildlife Conservation, and for Recreation and Tourism." In *Tropical Rain Forest Ecosystems*. Ed. F.B. Golley, H. Lieth and M.J.A. Werger. 325–334. Amsterdam, Netherlands: Elsevier Publishing, 1982.
- Myers, N. and Dorothy M. Myers. "From the 'Duck Pond' to the Global Commons: Increasing Awareness of the Supranational Nature of Emerging Environmental Issues." *Ambio*, 11/4 (1982), 195–201.
- Myers, N. "Room in the Ark?" Bulletin of the Atomic Scientists, 38/9 (1982), 44-48.
- —. "The Theory of Pleistocene Forest Refugia and Its Implications for Conservation in Africa and Other Parts of the Tropics." In *The Biological Model of Diversification in the Tropics*. Ed. G.T. Prance. 658–672. N.Y.: Columbia Univ. Press, 1982.
- -. "The Carbon Dioxide Connection." J. Social and Biological Structures, 6 (1983), 17-28.
- —. "Tropical Moist Forests: Over-Exploited and Under-Utilized?" Forest Ecology and Management, 6 (1983), 59–79.
- Myers, N. and E.S. Ayensu. "Reduction of Biological Diversity and Species Loss." Ambio, 12/2 (1983), 72–74.
- Myers, N. and Dorothy M. Myers. "How the Global Community Can Respond to International Environmental Problems." Ambio, 12/1 (1983), 20–26.
- Myers, N. "Depletion of Tropical Moist Forests: A Comparative Review of Rates and Causes in the Three Main Regions." Acta Amazonica, 12/4 (1983), 745–758.
- -. "A Priority-Ranking Strategy for Threatened Species?" The Environmentalist, 3 (1983), 97-120.
- Myers, N., Paul R. Ehrlich and 18 others. "Long-Term Biological Consequences of Nuclear War." Science, 222 (1983), 1293–1300.
- Myers, N. "The Tropical Forest Issue." In *Resource Management and Environmental Planning 4*. Ed. T. O'Riordan and R.K. Turner. 1–28. 1983.
- —. "A Wealth of Wild Species." Boulder, Colorado: Westview Press, 1983. Accepted as a Science book and a quality paperback of the Book of the Month Club, also by the Library of Science Book Club, the Natural Science Book Club, and the British Good Book Guide.
- -. "Wild Genetic Resources." Impact of Science on Society (UNESCO), 34/4 (1984), 327-334.
- -... "Genetic Resources in Jeopardy." Ambio, 13/3 (1984), 171-174.
- —. "Problems and Opportunities in Habitat Conservation." In Conservation of Threatened Natural Habitats. Ed. A.V. Hall. 1–15. Pretoria: South African National Scientific Programmes, 1984.
- —. "The Eternal Values of the Parks Movement and the Monday Morning World." In National Parks, Conservation and Development. Ed. J.A. McNeely and K.R. Miller. The Role of Protected Areas in Sustaining Society: 656–660. Washington, D.C.: Smithsonian Institution, 1984.

Myers, N., D.O. Hall and N.S. Margaris, ed. "Economics of Ecosystem Management." The Hague,

Netherlands: W. Junk Publisher, 1985.

- Myers, N., K.R. Miller and five others. "Issues in the Preservation of Biological Diversity." In *The Global Possible*. Ed. R. Repetto. Resources, Development and the New Century: 337–362. New Haven, Connecticut: Yale Univ. Press, 1985.
- Myers, N., J.M. Melillo and three others. "A Comparison of Recent Estimates of Disturbance in Tropical Forests." *Environmental Conservation*, 12 (1985), 37–40.
- Myers, N., R.A. Houghton and six others. "Net Flux of Carbon Dioxide from Tropical Forests in 1980." *Nature*, 316 (1985), 617–620.
- Myers, N. "Causes of Loss of Biological Diversity." Washington, D.C.: Office of Technology Assessment, U.S. Congress, 1985.
- -. "Tropical Deforestation and Species Extinctions." "The Latest News." Futures, 17 (1985), 451-463.
- —. "Forests and Environment." In Managing Global Issues. Ed. J.T. Kikhonen. 88–97. Finland: Univ. of Helsinki Press, 1985.
- —. "The Global Possible: What Can Be Gained?" In *The Global Possible*. Ed. R. Repetto. Resources, Development and the New Century: 477–490. New Haven, Connecticut: Yale Univ. Press, 1985.
- Myers, N., D.O. Hall and N.S. Margaris, ed. "Economics of Ecosystem Management." Dordrecht, Netherlands: W. Junk Publishers, 1985.
- Myers, N., "The End of the Lines." Natural History, 94 (1985), 2, 5, 12.
- —. "Environmental Repercussions of Deforestation in the Himalayas." J. World Forest Resource Management, 2 (1986), 63-72.
- —. "Tropical Forests: An Overview Assessment, With Impacts on Extinctions." In Conservation Biology: Science of Scarcity and Diversity. Ed. M.E. Soule. 394–409. Sunderland, Massachusetts: Sinauer, 1986.
- —. "Forestland Farming in Western Amazonia: Stable and Sustainable." Forest Ecology and Management, 15 (1986), 81–93.
- —. "Biological Resources of the Tropics." In Conservation for Productive Agriculture. Ed. V.L. Chopra and T.N. Khoshoo. 1–10. New Delhi, India: Indian Council of Agricultural Research, 1986.
- —. "Long-Term Impacts of a Nuclear Exchange on the Biosphere in Britain." In Civil Survival: 101–126. Oxford: Blackwell Books, 1986.
- Myers, N., J. Molofsky and C.A.S. Hall. "A Comparison of Tropical Forest Surveys." Carbon Dioxide Program. Washington, D.C.: Department of Energy, 1986.
- Myers, N. "Tree Crop-Based Agroecosystems in Java." Forest Ecology and Management, 17 (1986), 1-12.
- —. "Economics and Ecology in the International Arena: The Phenomenon of Linked Linkages." Ambio, 15 (1986), 296–300.
- -. "The Environmental Dimension to Security Issues." The Environmentalist, 6 (1986), 251-256.
- —. "Monitoring of Tropical Forests: The Role of Remote Sensing." Bilbao, Panama: Smithsonian Tropical Research Institute, 1986.
- -... "Tackling Mass Extinction of Species: A Great Creative Challenge." Albright Lecture in Conservation. Berkeley, California: Univ. of California, 1987.
- —. "Not Far Afield: U.S. Interests and the Global Environment." Washington, D.C.: World Resources Institute, 1987.
- Myers, N. and R. Tucker. "Deforestation in Central America: Spanish Legacy and North American Consumers." *Environmental Review*, 11 (1) (1987), 55–71.
- Myers, N. "Tropical Forests: Patterns of Depletion." In *Tropical Rain Forests and World Atmosphere*. Ed. G.T. Prance. 9–22. Boulder, Colorado: Westview Press, 1987.
- —. "Trends in the Destruction of Rain Forests." In Conservation in the Tropical Rain Forests. Ed. C.W. Marsh and R.A. Mittermeier. 3–20. N.Y.: Alan R. Liss, 1987.
- -. "The Extinction Spasm Impending: Synergisms at Work." Conservation Biology, 1 (1) (1987),

14-21.

- -... "Linking Environment and Security." Bulletin of the Atomic Scientists, 4 (8) (1987), 46-47.
- —. "Conservation of Africa's Cats: Problems and Opportunities." In *Cats of the World*. Ed. S.D. Miller and D.D. Everett. Biology, Conservation and Management. 437–446. Washington, D.C.: National Wildlife Federation, 1987.
- Myers, N., R.A. Houghton and 10 others. "The Flux of Carbon from Terrestrial Ecosystems to the Atmosphere in 1980 Due to Changes in Land Use: Geographic Distribution of the Global Flux." *Tellus*, 39B (1987), 122–139.
- Myers, N. "Emergent Aspects of the Environment: A Creative Challenge." *The Environmentalist*, 7 (3) (1987), 163–174.
- —. "Nature Conservation at a Global Level: The Scientific Issues." Inaugural Lecture for new Chair and Visiting Professorship. Netherlands: Univ. of Utrecht, 1987.
- Myers, N. and J.J. Kozub. "Land and Water Resources Management." *Economic Development Institute*. Washington, D.C.: World Bank, 1987.
- Myers, N. "Policy Issues for Environment and Development." New Economics, 1 (1987), 7-8.
- —. "Nuclear Winter in the Third World." In On the Brink: Nuclear Proliferation and the Third World. Ed. P. Worsley. 237–242. London: Third World Publications, 1987.
- —. "Population, Environment and Conflict." Environmental Conservation, 14 (1) (1987), 15–22. (Award for best paper of the year).
- —. "New Foods and Innovative Agriculture." In *The Right to Food: Technology, Policy and Third World Agriculture*. Ed. P. Ehrensaft and F. Knelman. 43–54. Montreal, Canada: Pharmi-Libri, 1988.
- --. "The Environmental Basis of Sustainable Development." Annals of Regional Science (Special issue on Environmental Management and Economic Development), 21 (1988), 33-43.
- -... "Tropical Deforestation and Remote Sensing." Forest Ecology and Management, 23 (1988), 215-225.
- -. "Tropical Forests: Much More than Stocks of Wood." J. Tropical Ecology, 4 (2) (1988), 208-220.
- —. "Tropical Moist Forests and Their Species: Going, Going...?" In *BioDiversity*. Ed. E.O. Wilson. 28–35. Washington, D.C.: Academy Press, 1988.
- —. "Philippines: Forestry, Fisheries and Agricultural Resource Management." Washington, D.C.: World Bank, 1988.
- —. "Draining the Gene Pool: The Causes and Consequences of Genetic Erosion." In Seeds and Sovereignty. Ed. J. Kloppenberg. Debate Over the Use and Control of Plant Genetic Resources. 90–113. Durham, North Carolina: Duke Univ. Press, 1988.
- —. "Tropical Forests: A Storehouse for Human Welfare." In *Tropical Rainforests, Diversity and Conservation*. Ed. F. Almeda and C.M. Pringle. 13–27. San Francisco: California Academy of Sciences, 1988.
- -... "Threatened Species: "Hot-Spots" in Tropical Forests." The Environmentalist, 8 (1981), 20.
- -. "Tropical Forest Species: Going, Going, Going." Scientific American, 259 (1988), 132.
- -... "Natural Resource Systems and Human Exploitation Systems: Physiobiotic and Ecological Linkages." Washington, D.C.: World Bank, 1988.
- -... "Environmental Degradation and Some Economic Consequences in the Philippines." Environmental Conservation, 15 (1988), 205-214.
- -. "Environmental Challenges: More Government or Better Governance?" Ambio, 17 (1988), 411-414.
- —. "Writing Off the Environment." In *The Business of Saving the World*. Ed. J. Elkington, T. Burke and J. Hailes. 190–192. London: Routledge Publishers, 1988.
- -. "Extinction Rates Past and Present." Bioscience, 39 (1989), 39-41.
- -. "Tropical Deforestation and Climatic Change." Environmental Conservation, 15 (1989), 293-298.
- -. "The Greenhouse Effect: A Tropical Forestry Response." Biomass, 18 (1989), 73-78.

- -. "Environment and Security." Foreign Policy, 74 (1989), 23-41.
- —. "Loss of Biological Diversity and Its Potential Impact on Agriculture and Food Production." In Food and Natural Resources. Ed. D. Pimentel and C. Hall. 49–67. N.Y.: Academic Press, 1989.
- —. "Tropical Forests and the Botanists Community." In Proc. of the XIVth Intl. Botanical Congress. Ed.
 W. Greuter and B. Zimmer. 291–300. Koenigstein, Germany: Koeltz Scientific Books, 1989.
- —. "The Future of Forests." In *The Fragile Environment*. Ed. L. Friday and R.A. Laskey. 22–40. Cambridge, U.K.: Cambridge Univ. Press, 1989.
- -... "Environmental Security: The Case of South Asia." Intl. Environmental Affairs, 1 (1989), 138-154.
- —. "A Mass Extinction Episode Ahead of Us: Predictable or Preventable?" In Conservation for the Twenty-First Century. Ed.D. Western and M. Pearl. 42–49. Oxford: Oxford Univ. Press, 1989.
- —. "Ecology of the Amazonian Rainforest." In Land Use Options for Amazonia Rainforests. Ed. C. Johnson, R. Knowles and M. Colchester. 9–12. Oxford: Oxford Univ. Press, 1989.
- —. "The Environmental Basis of Sustainable Development." In Environmental Management and Economic Development. Ed. G. Schramm and J.J. Warford. 57–68. Baltimore, Maryland: Johns Hopkins Univ. Press, 1989.
- ---. "Synergistic Interactions and Environment." Bioscience, 39 (1989), 506.
- -... "Nuclear Winter: Potential Biospheric Impacts in Britain." Ambio, 18 (1989), 449-453.
- —. "Tropical Deforestation and Climatic Change." In Climate and Geo-Sciences: A Challenge for Science and Society in the 21st Century. Ed. A. Berger, S.H. Schneider and J.C.L. Duplessy. 341–354. Dordrecht, Netherlands: Kluwer Academic Publishers, 1989.
- —. "Population Growth, Environmental Decline and Security Issues in Sub-Saharan Africa." In Environmental Stress and Security. Ed. A. Hjort af Ornas and M.A.M. Salih. 211–231. Uppsala, Sweden: Scandinavian Institute of African Studies, 1989.
- —. "Tropical Forests and Gaia." Forestry for Sustainable Development Program, College of Natural Resources, St. Paul, Minnesota: Univ. of Minnesota, 1989.
- —. "Tropical Forests for Sustainable Development." Forestry for Sustainable Development Program, College of Natural Resources. St. Paul, Minnesota: Univ. of Minnesota, 1989.
- —. "Sustainable Development: The Role of NGOs." Forestry for Sustainable Development Program, College of Natural Resources. St. Paul, Minnesota: Univ. of Minnesota, 1989.
- -. "Milieuconflikten Bedreigen Wereldvrede." Wetenschap und Samenleving, 41 (5) (1989), 5-11.
- —. "Natural Resource-Based Export Initiatives in Central America and the Caribbean." Commission for the Study of International Migration and Cooperative Economic Development. Washington, D.C.: U.S. Congress, 1990.
- —. "Economic Evaluation of Genetic Resources in Tropical Forests." Allgemeine Forst Zeitschrift fur Waldwirtschaft und Umweldtvorsorge, 1–2 (1990), 12–13.
- -. "Environment and Security: The Emergent Linkages." National Forum, 70 (1990), 30-31.
- --. "Tropical Forests." In Global Warming. Ed. J. Leggett. 372-399. Oxford: Oxford Univ. Press, 1990
- —. "Mass Extinctions: What Can the Past Tell Us about the Present and Future?" Global and Planetary Change, 82 (1990), 175–185.
- Myers, N. and D.W. Pearce. "Economic Values and the Environment of Amazonia." In *The Future of Amazonia*. Ed. D. Goodman and A. Hall. 383–404. London: Macmillan Press, 1990.
- Myers, N. "The Coming Challenge of Mass Extinction." In *Valuing Special Plants and Rare Species*. Ed. R.P. Cote. 5–14. Nova Scotia, Canada: Dalhousie Univ. Press, 1990.
- —. "Environmental Science and the Policy Interface: Facing Up to the Lack of Interface." In Sustainable Development, Science and Policy. 513–521. Oslo, Norway: Norwegian Research Council for Science and the Humanities, 1990.
- —. "The Biodiversity Challenge: Expanded Hot Spots Analysis." The Environmentalist, 10 (1990), 243–256.
- -... "The World's Forests and Human Populations: The Environmental Interface." In Resources,

Environment, Population: Present Knowledge, Future Options, Population and Development Review. Ed. K. Davis and M.S. Bernstam. (Special Supplement) 16 (1991), 233–247.

- —. "Man's Future Needs the Beasts." In Man and Beast. Ed. M. Robinson. 319–329. Washington, D.C.: The Smithsonian Press, 1991.
- —. "Biological Diversity and Global Security." In *Ecology, Economics, Ethics—The Broken Circle*. Ed. F. Bormann and S.R. Kellert. 11–25. New Haven, Connecticut: Yale Univ. Press, 1991.
- Myers, N., ed. "Tropical Forests: Present Status and Future Outlook." In *Climatic Change* (special issue on Tropical Forests and Climate), 19 (1–2) (1991), 3–32.
- Goreau, T.J. and N. Myers, ed. "Tropical Forests and the Greenhouse Effect: A Management Response." In *Climatic Change* (Special issue on Tropical Forests and Climate), 19 (1–2) (1991), 215–226.
- Myers, N. "Tropical Deforestation: the Latest Situation." BioScience, 41 (1991), 282.
- -. "Biologists as Policymakers?" Environmental Conservation, 18 (1991), 6.
- —. "Population, Resources and the Environment: The Critical Challenges." N.Y.: United Nations Population Fund, 1991. (French and Spanish translations.)
- -... "Population/Environment Linkages: Discontinuities Ahead?" Ambio, 21 (1992), 116-118.
- -. "Tropical Forests: The Policy Challenge." The Environmentalist, 12 (1992), 15-27.
- —. "The Anatomy of Environmental Action: The Case of Tropical Deforestation." In *The International Politics of the Environment*. Ed. A. Hurrell and B. Kingsbury. 430–454. Oxford: Oxford Univ. Press, 1992.
- —. "Synergisms: Joint Effects of Climate Change and Other Forms of Habitat Destruction." In Global Warming and Biological Diversity. Ed. R.L. Peters and T.E. Lovejoy. 344–354. New Haven, Connecticut: Yale Univ. Press, 1992.
- —. "The Environmental Consequences for the European Community of Population Factors Worldwide and within the Community." Brussels, Belgium: The European Commission, 1992.
- Myers, N., ed. "Tropical Forests and Climate." Dordrecht, Netherlands: Kluwer Academic Publishers, 1992.
- -... "Environment and Development: The Question of Linkages." BioScience, 43 (5) (1993), 302-309.
- -. "Questions of Mass Extinction." Biodiversity and Conservation, 2 (1993), 2-17.
- -. "Biodiversity and the Precautionary Principle." Ambio, 22 (2-3) (1993), 74-79.
- —. "Tropical Forests: The Main Deforestation Fronts." *Environmental Conservation*, 20 (1) (1993), 9–16.
- --- "Population, Environment and Development." Environmental Conservation, 20 (3) (1993), 1-12.
- -... "Environmental Refugees: How Many Ahead?" BioScience, 43 (11) (1993), 752-761.
- —. "Sharing the Earth with Whales." In *The Last Extinction*. Ed. L. Kaufman and K. Mallory. 179–194. Cambridge, Massachusetts: MIT Press, 1993.
- —. "Globale Umwelt Kooperation." In Jahrbuch Okologie. Ed. G. Altner, B. Mettler-Meibom, U.E. Simonis and E.U. von Weizsacker. 186–193. Munchen, Germany: Verlag CH Beck, 1993.
- Myers, N., P.R. Ehrlich and A.H. Ehrlich. "The Human Population Problem: As Explosive as Ever?" In Surviving with the Biosphere. Ed. N. Polunin and J.H. Burnett. 270–281. Edinburgh: Edinburgh Univ. Press, 1994.
- Myers, N. "Sub-Saharan Africa and Carrying Capacity." Environmental Awareness, 16 (1994), 125–135.
- —. "Protected Areas—Protected from a Greater What?" Biodiversity and Conservation, 3 (1994), 411–418.
- —. "We Do Not Want To Become Extinct: The Question of Human Survival." In *Biodiversity and Landscapes, A Paradox of Humanity*. Ed. K.C. Kim and R.D. Weaver. 133–150. N.Y.: Cambridge Univ. Press, 1994.
- -. "Global Biodiversity II: Losses." In Principles of Conservation Biology. Ed. G.K. Meffe and C.R.

Carroll. 110-140. Sunderland, Massachusetts: Sinauer, 1994.

- —. "Population Growth as a Factor Leading to Conflict over Land and Other Natural Resources." In Environment and Population Change. Ed. B. Zaba. 101–114. London: Ordina Editions, 1994.
- —. "Global Population and Emergent Pressures." In *Population and Global Security*. Ed. N. Polunin and M. Nazim. 17–48. Geneva, Switzerland: The Foundation for Environmental Conservation, 1994.
- —. "Tropical Deforestation: Rates and Patterns." In *The Causes of Tropical Deforestation*. Ed. K. Brown and D.W. Pearce. 27–40. London: Univ. College London Press, 1994.
- -... "Population Summit: Guest Editorial." Environmental Conservation, 20 (1994), 291-292.
- --. "Population and the Environment: The Vital Linkages." In *Population, Environment and Development*. 55-63. N.Y.: United Nations, 1994.
- —. "Future Operational Monitoring of Tropical Forests: An Alert Strategy." ISPRA Joint Research Centre. Varese, Italy: Commission of the European Community, 1994.
- -. "The World's Forests: Need for a Policy Appraisal." Science, 268 (1995), 823-824.
- -... "Environmental Unknowns." Science, 269 (1995), 358-360.
- —. "Tropical Deforestation: Population, Poverty and Biodiversity." In *The Ecology and Economics of Biodiversity Decline, The Forces Driving Global Change*. Ed. T. Swanson. 111–122. U.K.: Cambridge Univ. Press, 1995.
- --. "Population and Biodiversity." Ambio, 24 (1) (1995), 56-57.
- -. "Biodiversity." Environmental Awareness, 18 (1995), 51-60.
- —. "Economics of the Environment: A Seismic Shift in Thinking." Ecological Economics, 15 (2) (1995), 125–128.
- —. "Global Population Growth as a Source of Conflict." Center for International Studies, Pittsburgh, Pennsylvania: Univ. of Pittsburgh, 1995.
- Myers, N. and J. Kent. "Environmental Exodus: An Emergent Crisis in the Global Arena." Washington, D.C.: The Climate Institute, 1995.
- Myers, N. "The Rich Diversity of Biodiversity Issues." In *Biodiversity II*: Understanding and Protecting Our Natural Resources. Ed. M.L. Reaka-Kudla, D.W. Wilson and E.O. Wilson. 125–138. Washington, D.C.: National Academy Press, 1996.
- —. "Extinction and Biodiversity." In *The Physical Geography of Africa*. Ed. W.M. Adams, A.S. Goudie and A. Orme. 356–366. Oxford: Oxford Univ. Press, 1996.
- —. "Environmental Services of Biodiversity." Proc. of U.S. National Academy of Sciences, 93 (1996), 2764–2769.
- -... "The Biodiversity Crisis and the Future of Evolution." The Environmentalist, 16 (1996), 37-47.
- —. "Global Population Growth." In *Global Security Beyond 2000*. Ed. W. Burros. 25–26. Center for West European Studies. Pittsburgh, Pennsylvania: Univ. of Pittsburgh, 1996.
- Myers, N., ed. "Biodiversity: Environmental Discontinuities and Ecological Synergisms." *Biodiversity* and Conservation (Special issue on Discontinuities and Synergisms), 5 (1996), 1025–1034.
- --. "The World's Forests: Problems and Potentials." Environmental Conservation, 23 (1996), 156-168.
- -. "Development, Environment and Health: What Else We Should Know." Environment and Development Economics, 2 (1) (1997), 367-371.
- -... "Biodiversity's Genetic Library." In Nature's Services: Societal Dependence on Natural Ecosystems. Ed. G.C. Daily. 255-273. Washington, D.C.: Island Press, 1997.
- —. "The World's Forests and Their Ecosystem Services." In Nature's Services: Societal Dependence on Natural Ecosystems. Ed. G.C. Daily. 215–235. Washington, D.C.: Island Press, 1997.
- -... "Consumption: Challenge to Sustainable Development." Science, 276 (1997), 53-57.
- —. "Consumption in Relation to Population, Environment and Development." The Environmentalist, 17 (1997), 33–44.
- --. "Marine Fisheries: Two Macro-Constraints." Environment and Development Economics, 2 (1)

(1997), 88-93.

- ---. "Mass Extinction and Evolution." Science, 278 (1997), 597-598.
- -... "Environmental Refugees." Population and Environment, 18 (5) (1997), 509-524.
- —. "Perverse Subsidies: Their Nature and Extent." Chicago, Illinois: Research Report for the MacArthur Foundation, 1997.
- —. "Our Forestry Prospect: The Past Recycled or a Surprise-Rich Future?" The Environmentalist, 17 (1997), 233–247.
- —. "Global Biodiversity II: Losses and Threats." In Principles of Conservation Biology. Ed. G.K. Meffe and C.R. Carroll. 123–158. Sunderland, Massachusetts: Sinauer, 1997.
- —. "The Population/Environment Predicament: Even More Urgent than Supposed." Politics and the Life Sciences, 16 (2) (1997), 211–213.
- —. "The Biodiversity Challenge." In *The Human Impact Reader*. Ed. A. Goudie. 432–446. Oxford: Blackwell Academic Publishers, 1997.
- —. "Global Survival: A Convergence of Faith and Science?" In Ethics and Values—A Global Perspective. Ed. I. Serageldin and J. Martin-Brown. 22–25. Washington, D.C.: World Bank, 1997
- —. "Emergent Issues of Environmental Economics: What We Should be Analysing Closely But Haven't Thought Enough About." Intl. J. Social Economics, 25 (6/8) (1998), 1271–1278.
- —. "Global Population and Emergent Pressures." In Environmental Challenges II: Population and Global Security. Revised and updated edition. Ed. N. Polunin. 17–46. Cambridge, U.K.: Cambridge Univ. Press, 1998.
- —. "Global Conservation Priorities and Future Investment Policies." In Conservation in a Changing World: Integrating Processes into Priorities for Action. Ed. G.M. Mace, A. Balmford and J.R. Ginsberg. 273–285. Cambridge, U.K.: Cambridge Univ. Press, 1998.
- —. "Disappearing Species: Problems and Opportunities." In Proc. of the Royal Institution of Great Britain, 69 (1998), 169–194. Oxford: Oxford Univ. Press.
- —. "An Age of Environmental Opportunity." In *Revelation and the Environment*. Ed. S. Hobson and J. Lubchenco. AD 95–1995. 58–61. London: World Scientific Publishers, 1998.
- Myers, N. and J. Kent. "Perverse Subsidies: Tax \$s Undercutting Our Economies and Environments Alike." Winnipeg, Canada: International Institute for Sustainable Development, 1998. (Italian translation, Rome: Edizione Ambiente.)
- Myers, N., R.A. Mittermeier, et al. "Biodiversity Hotspots: A Focused, Species-Based Approach to Conservation Priorities." *Conservation Biology*, 12 (3) (1998), 516–520.
- Myers, N. "Lifting the Veil on Perverse Subsidies." Nature, 392 (1998), 327-328.
- —. "Natural Resources Conservation and Enhancement: Components of Ecotechnology." In Ecotechnology and Shaping the Future. Ed. M.S. Swaminathan. 21–24. Chennai, India: Madras Editorial Services, 1998.
- -.. "Population: Some Overlooked Issues." The Environmentalist, 18 (1998), 135-138.
- —. "What's This Biodiversity and What's It Done for Us Today?" In Scientists on Biodiversity. Ed. L. Kobner, J.E.S. Sokolow, F.T. Grifo and S. Simpson. 5–8. N.Y.: American Museum of Natural History, 1998.
- —. "The Next Green Revolution: Its Environmental Underpinnings." Current Science, 76 (4) (1999), 507–513.
- —. "Saving Biodiversity and Saving the Biosphere." In *The Living Planet in Crisis*. Ed. J. Cracraft and F. Grifo. 237–254. N.Y.: Columbia Univ. Press, 1999.
- —. "Population, Gender, Environment and Food Security." In Malthus and Mendel: Population, Science and Sustainable Food Security. Ed. M.S. Swaminathan. 69–74. Chennai, India: Madras Editorial Services, 1999.
- -. "Esodo Ambientale: Popoli in Fuga da Terre Difficili." Milan, Italy: Edizioni Ambiente, 1999.
- -. "Population Dynamics and Food Security." In Food Security: New Solutions for the 21st Century.

Ed. A.E. el Oebeid, S.R. Johnson, H.H. Jensen and L.C. Smith. 176–208. Ames, Iowa: Iowa State Univ. Press, 1999.

-... "Environmental Scientists: Advocates as Well?" Environmental Conservation, 26 (1999), 163–165.

- Myers, N., R.A. Mittermeier, P.R. Gil and C.G. Mittermeier. "Hotspots: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions." Monterrey, Mexico: CEMEX, Conservation International and Agrupacion Sierre Madre, 1999. Outside Mexico, Chicago, Illinois: Univ. of Chicago Press.
- Myers, N. "Perverse Subsidies." President's Lecture to the Royal Society of Arts, London. RSA J., 3–4 (1999), 85–91.
- Myers, N. and J. Kent. "Food and Hunger in Sub-Saharan Africa." Washington, D.C.: Report to the Winslow Foundation, 2000.
- Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca and J. Kent. "Biodiversity for Conservation Priorities." *Nature*, 403 (2000), 853–858.
- Myers, N. "Sustainable Consumption." Editorial in Science, 287 (2000), 2419.
- --. "The Meaning of Biodiversity Loss." In *Nature and Human Society: The Quest for a Sustainable World.* Ed. P.H. Raven. 63–70. Washington, D.C.: National Academy Press, 2000.
- -... "The New Millennium: An Ecology and an Economy of Hope." Current Science, 78 (2000), 686-693.
- —. "Sustainable Consumption: The Meta-Problem." In Towards Sustainable Consumption: A European Perspective. Ed. R.B. Heap and J. Kent. 5–15. London: The Royal Society, 2000.
- -. "Subsidies are "Perverse." World Water Watch, 1 (1) (2000), 42-43.
- —. "The Management and Repercussions of Nuclear Power." Oxon., U.K: The Ditchley Foundation, Enstone, 2000.
- —. "The Century Ahead: Ever-Greater Problems or Ever-Wider Opportunities?" United Nations Chronicle, 3 (2000), 8–11.
- -. "What's This Biodiversity and What's It Done for Us Today?" In *The Biodiversity Crisis: Losing What Counts*. Ed. M.J. Novacek. 22–62. N.Y.: The New Press, 2001.
- Myers, N. and J. Kent. "Food and Hunger in Sub-Saharan Africa." *The Environmentalist*, 21 (1) (2001), 41–69.
- -. "Biodiversity and Water Subsidies." Zeist, Netherlands: WWF International, 2001.
- Myers, N. "Hotspots." *Encyclopedia of Biodiversity*, Vol. 3, 371–381. Washington, D.C.: Academic Press, 2001.
- Myers, N. and A. Knoll. "The Biotic Crisis and the Future of Evolution." Proc. of National Academy of Sciences, USA, 98 (10) (2001), 5389–5392.
- Myers, N. and J. Kent. "New Consumers: The Influence of Affluence." Washington, D.C.: Report to the Winslow Foundation, 2001.
- Myers, N. "The World's Forests." In A Survey of Sustainable Development: Social and Economic Dimensions. Ed. J.M. Harris, T.A. Wise, K.P. Gallagher and N.R. Goodwin. Washington, D.C.: Island Press, 2001.
- —. "The Biodiversity Outlook: Endangered Species and Endangered Ideas." In Social Order and Endangered Species Preservation. Ed. J.F. Shogren and J. Tschirart. N.Y.: Cambridge Univ. Press, 2001. (In press)
- —. "Environmental Refugees." Encyclopedia of Global Environmental Change, Vol. 3. Chichester, U.K.: John Wiley, 2001. (In press)
- —. "Environmental Refugees: Our Latest Understanding." Philosophical Transactions of the Royal Society B., 2001. (In press)
- Myers, N. and S.L. Pimm, et al. "Can We Defy Nature's End?" Science, 2001. (In press).
- Myers, N. "Sustainable Development: Tackling Problems—Or Sources of Problems?" In Proc. of United Nations Univ. Conference. Ed. J. von Ginkel. Sep. 3–4, Tokyo, Japan: 2001. (In press).

- --. "Mediterranean-Climate Regions: Glowing Hotspots of Diversity." J. Mediterranean Ecology, 2002. (In press)
- -... "Biodiversity and Biodepletion: The Need for a Paradigm Shift." In *Protecting the Protected: Managing Biodiversity for Sustainability*. Ed. S. Stoll and T. O'Riordan. Cambridge, U.K.: Cambridge Univ. Press, 2002. (In press).

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