



Blue
Planet
Prize

FOR IMMEDIATE RELEASE

June 12, 2001

**2001 BLUE PLANET PRIZE:
ANNOUNCEMENT OF PRIZE WINNERS**

Sir Robert M. May (Australia)

For developing mathematical ecology and the fundamental tools for ecological conservation planning.

Dr. Norman Myers (United Kingdom)

For being the first to warn of mass species extinction and for continuing to speak out about environmental problems.

The Asahi Glass Foundation (Chairman Hiromichi Seya) has announced the recipients of the 10th Blue Planet Prize, an international environmental award. The Blue Planet Prize is awarded annually to two individuals or organizations that have made outstanding scientific contributions to global environmental conservation.

The following individuals were selected as the recipients of the Blue Planet Prize for 2001.

Sir Robert M. May established statistical methods for tracking and estimating species populations based on mathematical models, thereby providing the basic tools for planning ecological preservation efforts ranging in scope from the local to the global. He has not limited his approach to animals. His mathematical models are also widely applied in studies of disease transmission caused by microorganisms, such as bacteria.

Dr. Norman Myers works as an independent scientist. He was the first to alert the world to the mass extinction of species underway, and to spell out action responses to both species loss and the associated problem of tropical deforestation. In addition, he has warned of fundamental challenges such as the intertwined issues of environmental conservation and economic development.

The recipients will be awarded certificates of merit, commemorative trophies and supplementary awards of 50 million yen.

The award ceremony will be held on Thursday November 15, 2001, at the Hotel New Ohtani in Tokyo (Chiyoda-ku,) which will be followed the next day by commemorative lectures delivered by the recipients at the United Nations University in Tokyo (Shibuya-ku)

(For further information about the winners, please see the attachment.)



For more information, please contact: **Nobuaki Kunii**

THE ASAHI GLASS FOUNDATION

2nd Floor Science Plaza, 5-3 Yonbancho Chiyoda-ku, Tokyo 102-0081 Japan

Phone +81 3 5275 0620 Fax +81 3 5275 0871

E-Mail: post@af-info.or.jp URL: <http://www.af-info.or.jp>

Printed on recycled paper

Remarks from the Award Recipients upon Being Notified of Their Selection

Sir Robert M. May

“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.

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?

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. So I am hugely pleased to accept the 2001 Blue Planet Prize which recognizes the vital importance of this general subject.”

Dr. Norman Myers

“I am deeply grateful to the Asahi Glass Foundation for awarding me this prestigious prize. I am specially gratified because I pursue environmental science in a way different from most of my colleagues around the world. I work on my own. This has many advantages but also its drawbacks. Your generous award will enable me to carry on with my independent career in a much more productive manner than hitherto. I can now concentrate on what I view as the most important environmental questions of our time. I feel you are setting me free to do more in the next decade than in all my professional life to date.

I am also grateful that you have recognized me for work that spans a range of environmental fields. I specialize in being a generalist, which, like my independent status, is far different from what most scientists do and is rarely recognized through a top rank prize. Your award will send a strong message to start-out scientists who will be encouraged to undertake the kinds of interdisciplinary work that are sorely needed if we are to measure up to our environmental challenges. Your Prize will similarly encourage those same young scientists to take their scientific findings and policy recommendations to political leaders and others in the public arena—where they certainly belong.”

Profiles of the 2001 Blue Planet Prize Recipients

Sir Robert M. May

Sir Robert obtained his doctorate in theoretical physics from the University of Sydney at the age of 23 in 1959, researching that field there for the next 13 years until in due course he switched disciplines to population biology at Princeton University in the United States, where he remained a further 15 years. In 1988, he moved to Oxford University in the United Kingdom and solidified his position as a world leader in mathematical biology. Since 1995, he has been Chief Scientific Adviser to the British Government and Head of the Office of Science and Technology, playing an influential role in national scientific affairs.

Applying the mathematical concepts nurtured in theoretical physics to the field of biology, in 1973 he authored "Stability and Complexity in Model Ecosystems," a book that used mathematical modeling to investigate the stability and complexity of a community of interacting plants and animals following the foodweb as clue. Contrary to the general understanding that species are motivated toward greater stability in complex ecosystems, he showed in population dynamics models that individual species are liable to greater fluctuations in abundance in such ecosystems when the number of species is increased and species interactions are randomly added. Since the publication of this research, Sir Robert has accumulated a solid record of noteworthy accomplishments in the field of mathematical biology.

Sir Robert was also the first to discover that, first-order nonlinear difference equations can exhibit an astonishing array of dynamical behavior, ranging from stable points to apparently random or "chaotic" fluctuations. Although chaos theory itself was discovered independently by several mathematicians at about the same period of time, it was Sir Robert's research, beginning with his article published in "*Nature*" in 1976, that can be credited with creating the new field of "chaotic dynamics" in biology.

One of Sir Robert's major contributions was to be the first to build a model that includes environmental stochasticity and spatial heterogeneity in studies of population dynamics, and thereby contributing to our ability to formulate environmental policies. He also drew attention to these characteristic changes in populations for the purposes of managing ecosystems. For example, in collaboration with others he has explored the ways fish harvesting affects multispecies ecosystems of the fishing grounds. "*Exploitation of Marine Communities*" reports the results of this work. He has also contributed importantly to understand the cyclic oscillations exhibited in insect parasitoid populations in the wild, demonstrating through mathematical models the relationship between the ecology of predatory parasites, such as parasitic wasps, and population numbers, which matched the actual observations in the wild.

In the last 10 years, Sir Robert, who has continued fundamental research into mathematical biology and sought policies that can be applied to the resolution of environmental problems, has played a leading role in two areas of research in particular. The first combines mathematical and applied techniques to analyze the conditions under which viruses and bacteria affect host populations and their distribution. The results obtained in these studies have been beneficial to a broad spectrum of science in the public health sector, ranging from genetic research into groups of disease carriers to immunology for rubella in the UK and to strategies for dealing with parasites. In addition, he is

investigating the conditions under which AIDS spreads, utilizing a combination of simplified analytical models and computer simulations to provide the data required to predict the spread of this disease.

The second area of concentration is research into the detailed reasons why the biodiversity of tropical regions is so extensive. He is studying the time and geographic factors in changes in biodiversity. The mathematical biology methodology he has developed are being used to measure this diversity, and make it possible to infer changes in that diversity, thereby increasing understanding of the composition and collapsing of biodiversity.

Sir Robert has used his mathematical modeling to explain the current state of biodiversity and warn that the risk of species extinction is currently at an historical high. He continues to strongly advocate the necessity of responding immediately to this crisis. He is presenting proposals and advice to governments and NGOs and making a real contribution toward the formulation of environmental conservation policies. He is also proffering effective proposals for policies to deal with contagious diseases, such as AIDS, based on his mathematical projections of the epidemiology.

His accomplishments have already been widely recognized in the United Kingdom and abroad. In 1995, he was named the Chief Scientific Advisor to the UK Government and was knighted the following year. In 2000, he was appointed President of the Royal Society of London, a position with a rich tradition and one of the most esteemed in the world of science. He is making good use of this elite standing to promote solutions to a wide range of issues, including ecological preservation, other urgent environmental problems such as global warming, and various problems related to medicine and biology.

Education and Academic and Professional Activities

1936	Born on January 8 in Australia
1956	Graduates from Sydney University
1959	Obtains his Doctorate (Theoretical Physics, Sydney University)
1959-1961	Researcher, Harvard University, U.S.A.
1962-1972	Professor, Sydney University (Physics)
1973-1988	Professor, Princeton University (Biology)
1988-1995	Professor, Imperial College and Oxford University, United Kingdom
1995-2000	Chief Scientific Advisor to the Government of the United Kingdom
2000 ~	President, Royal Society of London in December

Major Awards Received

1979	Fellow of The Royal Society of London
1980	Weldon Memorial Prize (Oxford University)
1984	MacArthur Award
1991	The Linnean Society's Linnean Medal
1991	Overseas Member, Australian Academy of Sciences
1992	The Inaugural Christian Marsh Prize
1992	Foreign Member of the US National Academy of Science
1995	Zoological Society Frink Medal
1996	Crafoord Prize in Biosciences (Sweden)
1998	Balzan Prize (awarded by the President of Italy)

Dr. Norman Myers

After graduating from Oxford University in 1958, Dr. Myers spent 12 years researching wildlife in Africa before earning his doctorate in the United States in 1973. He has taught at a number of renowned universities on both sides of the Atlantic, including Oxford and Harvard. He has served as an adviser to many governments, international agencies and academic bodies. One of the chief characteristics of his research is his penchant for raising new questions as well as supplying new answers to established questions. To date, he has pioneered 15 research issues.

In the early 1970s the rate of species extinction was officially considered to be around one species per year. Dr. Myers calculated that it was likely to be as high as one species per day. If the extinction rate were to continue at that pace alone, it would precipitate the wholesale demise of species. Through more detailed research in the late 1980s and as tropical forests disappeared faster than ever—these forests feature the bulk of all species—he increased his extinction estimate to roughly 50 species per day. He also noted that the “natural” extinction rate before humans arrived was roughly one species every 3-5 years. Although his findings were severely criticized at first, most scientists have eventually come to accept them. In the late 1990s he has demonstrated that the current biotic crisis will not only eliminate large numbers of species, but it will destroy several major “powerhouses” of evolution, notably tropical forests and wetlands, these being the principal sources of new species in the wake of mass extinctions in the prehistoric past. The crisis will also deplete certain other basic processes of evolution. All in all, it will leave an impoverished planet for millions of years into the future—unless we take vigorous action forthwith.

Toward the end of the 1970s, Dr. Myers predicted that the rapidly accelerating decline of tropical forests, at approximately 75,000 square kilometers per year, could well double within another decade. Once again there were many critics of this conclusion, but he was ultimately proven correct through latest satellite imagery. In the early 1980s Myers was the first to warn that deforestation in Central America was mainly due to conversion of forests into cattle pastures to supply cheap beef for North America’s fast food industry—a destructive process that he labeled the “hamburger connection”, showing the international linkages of environmental decline. In similar style he drew attention to tropical forests’ influence on climate both locally and globally.

Also in the early 1980s Dr. Myers documented the economic value of species and their genetic resources as start-point materials for pharmaceuticals including anti-cancer drugs, new foods, natural pesticides, and raw materials for industry ranging from oils and gums to plastics and latexes.

In the late 1980s Dr. Myers concluded that a sound way to conserve threatened species was to concentrate on “biodiversity hotspots”, being areas where exceptional concentrations of endemic species are undergoing exceptional loss of habitat. In the late 1990s he and colleagues calculated that at least one third of all species are confined to 25 hotspots comprising just 1.4% of earth’s land surface. He proposed that if these hotspots were preserved, the mass extinction ahead could be greatly reduced. His original analysis has been adopted by conservation organizations generating \$550 million to date, the largest sum ever assigned to a single conservation strategy.

Dr. Myers’ expertise in both the natural sciences and the social sciences has enabled him to contribute responses to a broad range of environmental issues, including population pressures, developing country poverty, over-consumption, unsustainable agriculture, climate change and environmental security. In a 2001 book, for example, he has presented a superb quantitative analysis of “perverse”

subsidies, being subsidies that damage both our economies and our environments. These subsidies amount to as much as \$2 trillion worldwide each year in sectors such as agriculture, fossil fuels, road transportation, water, forestry, and fisheries. The subsidies are large enough to cause major distortion of our economies and to inflict grand-scale injury on our environments. As a response to his policy proposals, several governments are reducing their perverse subsidies.

In addition, Dr. Myers has been a senior advisor to organizations such as the United Nations, the World Bank, the White House, scientific academies in a dozen countries, and numerous Japanese corporations. This testifies to the high regard accorded to his innovative research. He has raised the awareness of influential politicians (including six prime ministers and presidents), leading policy makers, and business chiefs worldwide, notably with respect to the many linkages between environmental conservation and economic development.

Dr. Myers has publicized his work in more than 250 scholarly papers, plus 300 popular articles and 17 books (sales of these books, over one million copies). His efforts to raise an extended series of pioneering questions, together with proposals for integrating environmental imperatives into nation-wide policies, will help us to advance toward a sustainable future for both our earth and our world.

Education and Academic and Professional Activities

1934	Born on August 24 in the United Kingdom.
1958	Graduated with bachelor's degree, Oxford University
1958-1965	District Officer in the Kenya Administration, and 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	Earned doctorate from the University of California, Berkeley
1972-present	Research projects for the U.S. National Academy of Sciences and its National Research Council, the Royal Society in the United Kingdom, the Soviet Academy of Sciences, the U.S. Department of State, NASA, the World Bank, United Nations agencies, the OECD, The European Commission, the World Wide Fund for Nature, the World Resources Institute, and many other bodies. Honorary Visiting Fellow of Green College, Oxford University.

Major Awards Received

1983	Gold Medal, World Wildlife Fund
1986	Gold Medal, New York Zoological Society
1987	Special Achievement Award, the Sierra Club
1987	Distinguished Achievement Award, the 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 for the World Wide Fund for Nature/UK

Report on the Selection Process (10th Annual Prize, 2001)

A total of 1,100 nominators from Japan and 1,500 nominators from other countries recommended 136 candidates. The fields represented by the candidates, in order of numbers, were atmospheric and earth sciences (40), ecology (27), complex fields (14), and environmental ethics and philosophy, and restoration of environmental destruction (13).

The candidates were drawn from 29 countries, with those from developing countries numbering 23, or 17% of the total.

At a meeting of the Foundation's Board of Directors and Councillors, the Board formally resolved to award the Prize to Sir Robert M. May and Dr. Norman Myers after numerous screenings by the Selection Committee under consultation with the Presentation Committee, a subcommittee of the Board.



The contents of this press release may also be viewed at the Asahi Glass Foundation's Internet web site. Please visit us on-line at:

<http://www.af-info.or.jp>

Printed on recycled paper

Message to the Japanese Public

Sir Robert M. May

The previous century has seen more advance 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: for example, climate change and diminishing biological diversity. What happens to our world, and to us, 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.

Dr. Norman Myers

We live at an altogether unprecedented time in human history. Entire segments of our planetary ecosystem face terminal threat through mass extinction of species, tropical deforestation, 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 wellbeing too. Are we not a privileged generation to live at a stage in human history when we have opportunity to save both our earth and our world? We shall surely earn the thanks of numerous generations into the future.

The Winners of the Blue Planet Prize

2001

2001

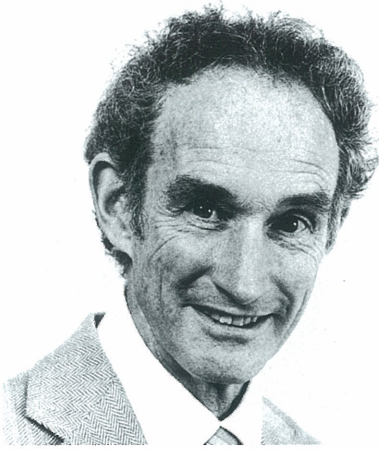
Blue Planet Prize

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

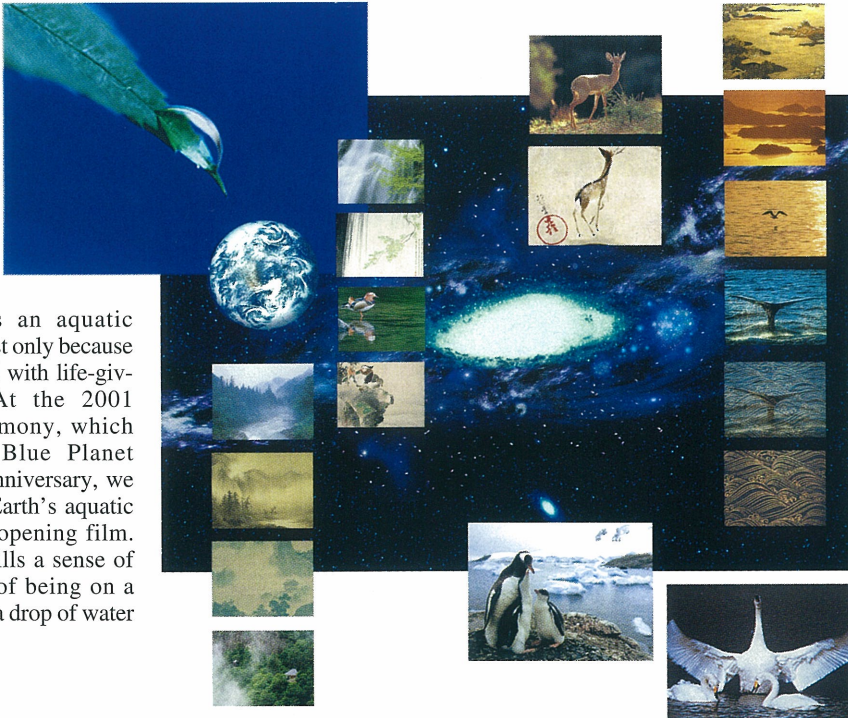
President of the Royal Society of London

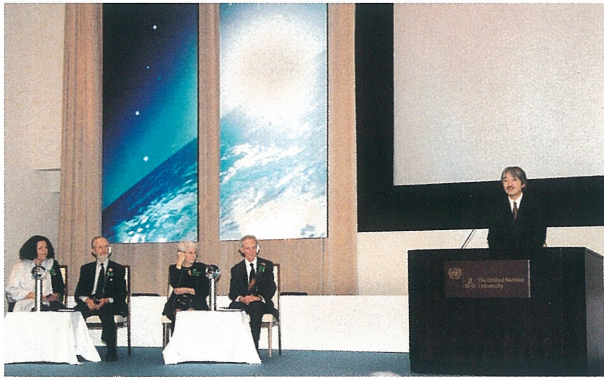
**Dr. Norman Myers
(U.K.)**

Honorary Visiting Fellow, Green College,
Oxford University



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

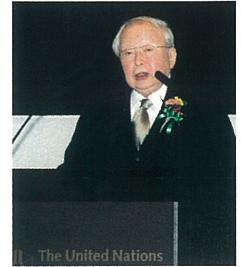




His Imperial Highness Prince Akishino at the ceremony.

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, Royal Society of London.

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

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

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

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

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

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

Lord (Robert) May of Oxford

February 2002

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

Numbers of Species Today

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

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

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

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

Understanding Diversity

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

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

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

individuals scale roughly linearly with area).

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

Extinction Rates

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

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

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

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

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

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

Why Value Biological Diversity?

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

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

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

Conclusion

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

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

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. Conserv.*, 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).

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

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

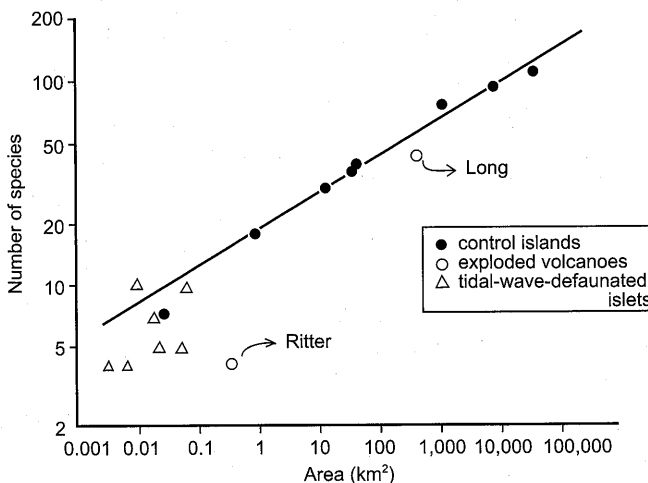


Figure 1. An example of the relation between species number and island area in an archipelago: number of resident, nonmarine, lowland bird species S on islands in the Bismarck Archipelago, plotted as a function of island area on a double logarithmic scale. The solid circles represent relatively undisturbed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

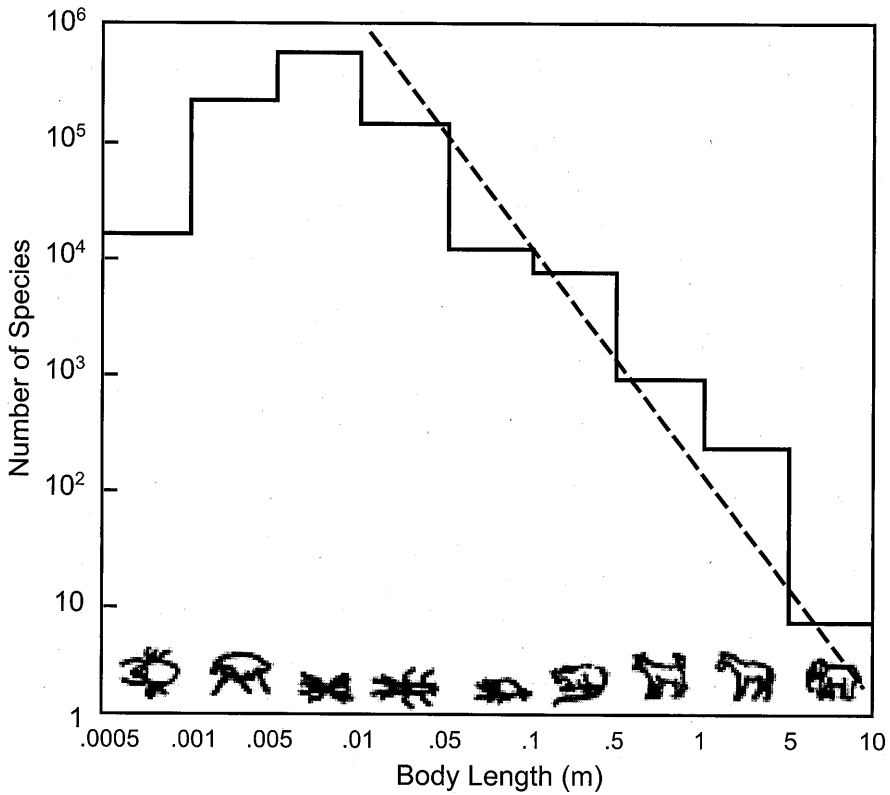


Figure 2. A crude estimate of the distribution of all terrestrial animals categorized according to characteristic length L . The dashed line indicates the relation $S \sim L^{-2}$, as in Fig. 3 (S = number of species). (After May, 1978)

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

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

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

Dynamics of Plant and Animal Populations

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

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

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

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

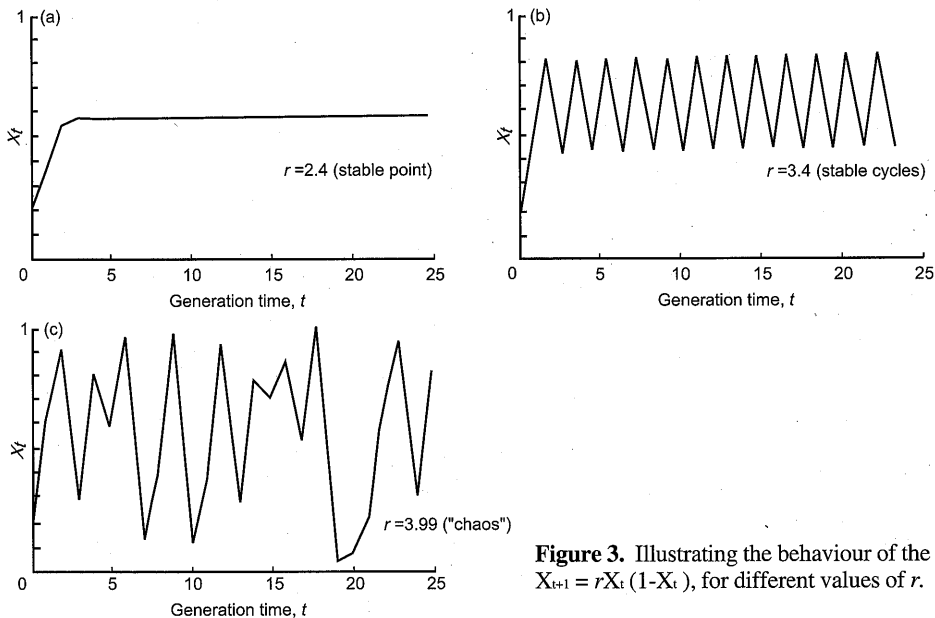


Figure 3. Illustrating the behaviour of the equation $X_{t+1} = rX_t(1 - X_t)$, for different values of r .

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

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

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

Biodiversity

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

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

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

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

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

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

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

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

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

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

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

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

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

EXTINCTION RATES

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

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

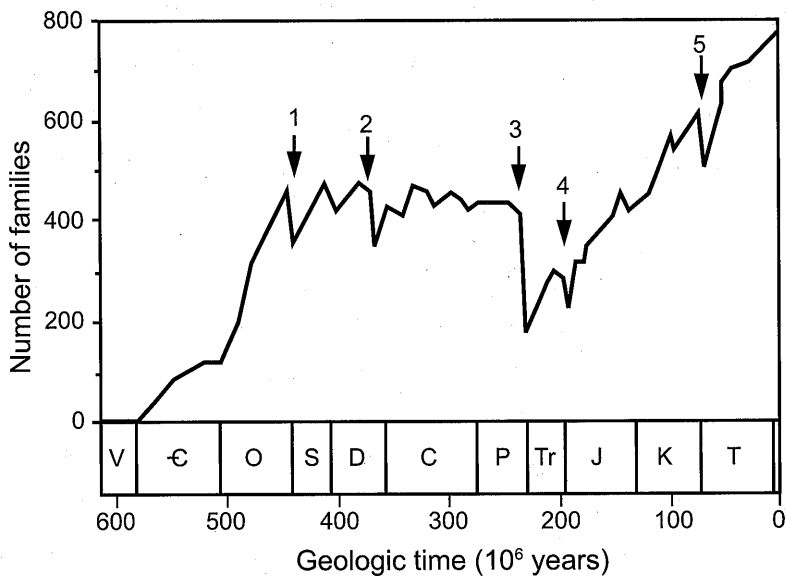


Figure 4. The history of the diversity of marine animal families, as shown by the fossil record over time. The curve connects 77 discrete data points, each giving the total number of well-skeletonized families from a particular stratigraphic stage. The arrows indicate the Big Five episodes of mass extinction.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

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

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

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

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

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

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

Why Value Biological Diversity?

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

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

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

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

Conclusion

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

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

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." *Biodiv. and Conserv.*, **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." *Nature*, **395**, 794–798.
- McKinney, M.L. 1998. "Branching Models Predict Loss of Many Bird and Mammal Orders within Centuries." *Anim. Conserv.*, **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 Verlag, 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: Springer-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. Cherratt. 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-Chavez, 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. Bohoeffter 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.” *Fortschritte 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. Biosci.*, 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. Dowlatbadi, 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 Biología." *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 Frágil 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. Cojocar 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. Pellow, 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. Pellow, 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." *Intr. 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. & Conserv.*, 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.