Lord Robert May of Oxford 1936–2020[*]

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Robert May was the leading theoretical ecologist of his generation. He started his career as a theoretical physicist and began the transition to ecology soon after completing a post-doctoral fellowship at Harvard. His mathematical analysis of the stability of ecological communities challenged orthodox views and spawned a new research agenda. He demonstrated that many different patterns of population fluctuations, including chaotic behaviour, could arise from simple mathematical models. Together with R. M. Anderson he transformed the mathematical modelling of infectious diseases. All of his work was characterised by his remarkable ability to reduce complex problems to their essential simplicities. His achievements were recognised by the award of numerous major international prizes. May also served as government chief scientific advisor (UK) between 1995 and 2000, and as president of the Royal Society between 2000 and 2005.

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Early years

Robert ('Bob') McCredie May (Fig. 1) was born on 8 January 1936 in Sydney, New South Wales, Australia. His paternal grandfather, who ran a pharmaceutical wholesale business near Carrickfergus, Northern Ireland, had left abruptly as a consequence of death threats from the Irish Republican Army (IRA), when May's father was about fourteen years old. Bob's maternal great-grandfather had moved from Stranraer to work in Northern Ireland as a stonemason on the Lanyon Building at Queen's University, Belfast. The family subsequently moved to Australia and became prosperous builders and quarry owners, although by the time May was born the money had largely dissipated.

May's parents met through a local Presbyterian church in Sydney. His father started out as a successful barrister, but quite early in his career became an alcoholic, as a result of which he was divorced by May's mother when May was seven years old. May subsequently hardly ever met his father and was aged just seventeen when he last saw him. This left a permanent mark on May's outlook: he was a teetotaller and to the end of his life was ambivalent about his father, on the one hand never forgiving him for being an alcoholic, on the other, admiring his talent as a lawyer and often recounting that he had been one of the smartest of his generation.

May's only sibling, his surviving younger brother Ron (Fig. 2), a talented athlete, worked as a senior economist at the Reserve Bank of Australia. Having been posted to Port Moresby in Papua New Guinea (PNG), where the bank had an office, in his spare time he assembled a substantial collection of cultural artefacts. He soon switched jobs to head the Australian National University Field Station and became an academic expert on the history, culture and politics of PNG and other Pacific countries.

May's mother was both a strict disciplinarian and protective towards her sons. Bob suffered from asthma, and as a result missed a lot of school as a young boy, and was not allowed to join others in

Fig. 1. The portrait photograph was taken in 1985 for the Royal Society and is © Godfrey Argent Studio.

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Fig. 2.   Bob and Ron (photograph courtesy of Mrs Judith May).

certain activities such as swimming. He was, by his own account a rather solitary child, a voracious reader, and 'inhabited the world of imagination'.[1] During the early years of World War 2, he was taught by his mother and two great aunts, who had been missionaries in India and lived in the Blue Mountains west of Sydney, before he moved back to the city to complete his primary and secondary school education.

The family was Scottish Presbyterian and, although by the age of about twelve May had decided he was not a believer, his social life revolved around the church and he led the local Presbyterian youth fellowship, taught bible classes and even preached a couple of sermons as well as becoming the table tennis champion of the youth fellowship.

Young May began to show his exceptional intellectual, and in particular his mathematical, prowess at Sydney Boys High School, a selective state school. He remained very proud of the school, saying it 'had wonderful teachers' and that he had a 'wonderful time' there. His performance in his high school mock graduation exams showed how far ahead of his peers he stood: he scored ~784 out of 800, ~100 marks clear of the next boy. May said that he found exams very easy and his stellar performance was a kind of 'party trick'.

Student at the University of Sydney

The person who influenced May most at Sydney Boys High was his chemistry teacher, Lenny Basser. May reported that seven of Basser's pupils went on to be elected Fellow of the Royal Society

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[1] The 'account' is the interview with May conducted by Robin Williams, from which quotations and other information in this memoir are drawn. Williams (2008).
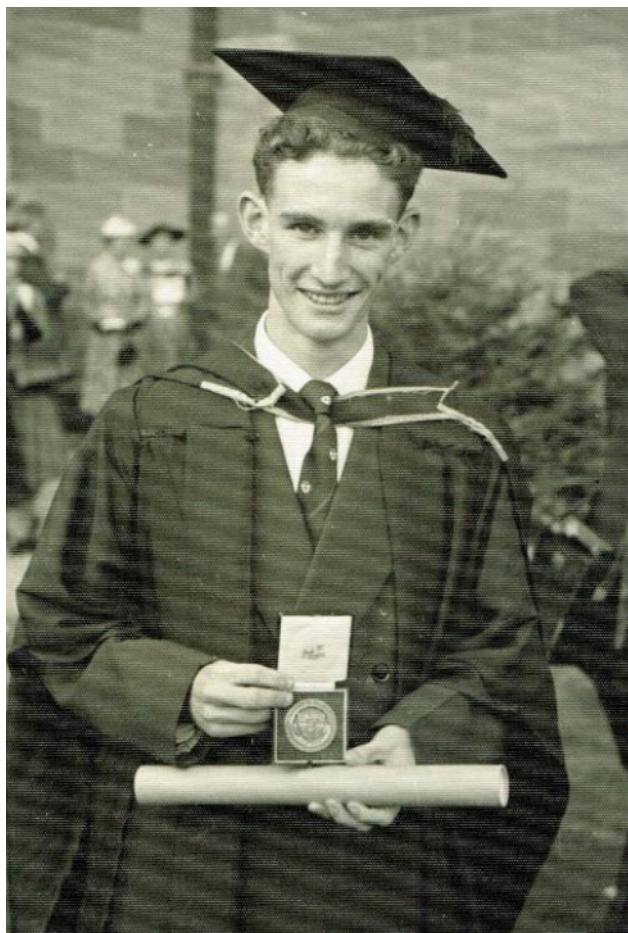
Fig. 3. Graduating from the University of Sydney (photograph courtesy of Mrs Judith May).

(FRS), three to the United States National Academy of Sciences and one won a Nobel Prize. It was at Basser's suggestion that May decided to study chemical engineering at the University of Sydney (Fig. 3). He greatly enjoyed student life, found a congenial set of friends, and played a lot of chess and snooker, though he found the practical side of chemistry and the long hours in the laboratory rather time-consuming.

First year chemical engineering involved classes in mathematics, chemistry and physics, and while May did the honours courses in the first two he only signed up for pass degree level physics. But when the exams came, on a whim he also took the honours physics exam (he claimed it was the last test and he had to hang around for his friends to finish before they all went to a party) and came top, winning a prize in chemistry and physics. But to claim the lucrative prize he had to do second-year physics, and this led to him coming to the attention of the head of physics, Harry Messel (1922–2015).[2]

Messel had been hired by the university to strengthen Sydney's physics department and he recruited a talented group of young physicists including Stuart Butler, John Blatt and Robert 'Robbie'

Schafroth. Messel spotted May's potential as a theoretical physicist and persuaded him to switch from engineering to science. May recalled making this decision knowing that he was giving up a safe vocational degree for the riskier career choice of academic science. The fact, obvious to May, that the Sydney physicists under Messel's inspirational leadership were having intellectual fun seems to have strongly influenced him. He described pure research as 'playing games with Nature in which the rules of the game are to try to work out what the rules are'. In his third year, May had to choose to major in pure mathematics, applied mathematics or physics, but against advice majored in all three, and came top in all three.

May remained at Sydney to do graduate work on superconductivity with Schafroth who had been a student and then assistant of Wolfgang Pauli. At the time, May said, there was a 'wonderful arrogance' among theoretical physicists and 'people felt that it would be possible to start a whole new area of solid state physics on a wet weekend'. Explaining superconductivity was then the outstanding problem in solid state physics and had been worked on by many of the greats of early twentieth-century physics including Albert Einstein. It was generally agreed that the solution would involve spin-1/2 electrons (fermions) pairing up in a way that would cause them to behave like spin-1 bosons. Critical to this realisation had been Schafroth's demonstration that a charged gas of bosons could be a superconductor, and May set to work on the theory of superconducting gases. But in his second year Bardeen, Cooper and Schrieffer produced a convincing microscopic theory of superconductivity based on the condensation at low temperature of 'Cooper-pairs' of electrons,[3] work for which they would later receive the 1972 Nobel Prize in Physics. There was still much to do in superconductivity, but the key problem had been solved.

Robbie Schafroth, whom May later described as 'a wonderful human being', accepted a chair in physics at Geneva and Bob planned to move with him to Switzerland in the fourth year of his PhD. But tragedy intervened; taking the opportunity to see the Australian interior before he left for Europe, Schafroth and his wife were killed in a light plane accident in May 1959. Bob was devastated, and over fifty years later still spoke of the shock of hearing the news: 'I just decided that I wanted to get out of Sydney as soon as I could after that'.

Postdoctoral studies at Harvard and transition to ecology

After completing his PhD thesis, which he described as 'mainly about why it didn't work', ('it' being calculations to underpin the Sydney idea for creating Cooper pairs), May arrived in October 1959 at Harvard as a postdoctoral fellow. He records that he did not write any papers, but worked with interesting people and, most importantly, met his future wife Judith, an undergraduate at Brandeis University, on a blind date. Although he was offered tenure-track positions in physics at Harvard, Chicago and Duke, May wanted to return to Australia and he accepted a senior lectureship in the physics department at the University of Sydney. Judith joined him after six months and they married in August 1962.

Back in Sydney, May, in his own words 'was doing ok but not particularly outstandingly' in physics, when, in 1968, he met the

ecologist Charles Birch through an organisation for social responsibility in science.[4] May had used some ecological examples to illustrate a course in mathematics for physicists, and Birch, although sceptical about the value of mathematics in ecology, arranged for May to contact ecologists in the United Kingdom (UK) and United States of America (USA), who were more sympathetic to mathematical modelling, in particular John Maynard Smith at the University of Sussex, Sir Richard Southwood at Imperial College, London and Robert MacArthur at Princeton University.

Shortly after, in 1970–1, May took an eighteen-month sabbatical, the first half of which he spent at Culham (at that time the UK Atomic Energy Authority Laboratory) from where he visited Southwood at the Imperial College Field Station, Silwood Park, and also met Michael Hassell and Sir Gordon Conway. This was the start of an enduring link with the Silwood group. He spent the second half of his sabbatical at the Institute for Advanced Study in Princeton, and used the opportunity to meet Robert MacArthur, the leading US theoretical ecologist at the time. The story goes that MacArthur arranged for the meeting to be curtailed after fifteen minutes by a colleague knocking on the door to call him away to an urgent phone call. The conversation with MacArthur apparently went very well, lasted much longer than fifteen minutes, and took an unexpected turn. MacArthur revealed that he had been diagnosed with terminal cancer, had less than a year to live, and was hoping to have a role in identifying his successor. He asked May whether or not he was interested. May replied that he was returning to Sydney, and MacArthur asked him to think over the offer.

During the first six months after returning to Australia, May wrote his first major contribution to theoretical ecology, a book entitled *Stability and Complexity in Model Ecosystems*[5] (see section below) and soon after started to explore the chaotic behaviour of non-linear difference equations that were used by ecologists in modelling population dynamics (see below). May summarised the situation like this: 'At the end of six months it was clear there were more and more problems because I had blundered into ecology at just the time when the subject, which had been purely descriptive, was making the transition to acquiring a conceptual base'.

In 1973, May moved to Princeton University to become MacArthur's successor as Class of 1877 Professor of Zoology, and he spent the next sixteen years of his career there, including eleven years as vice president for research. Throughout this period, he made regular summer visits to Southwood's group at Imperial College where he met new colleagues, including Sir Roy Anderson, and Sir John Lawton and Sir John Beddington (both then at the University of York), with whom he developed long-term scientific and social relationships.[6]

In 1979, Southwood moved from Imperial to become the head of the Department of Zoology at Oxford. The department had a very distinguished history at that time, with many Fellows of the Royal Society and a recent Nobel Prize winner, Niko Tinbergen, but most of these individuals had either retired or died, and Southwood set about building a new generation of scientific leaders. By the late 1980s, when he persuaded May to move to Oxford (in a post shared with Imperial) as a Royal Society Research Professor, the department was host to one quarter of all the holders of these prestigious posts.

Population ecology

Ecologists seek to explain the distribution and abundance of living organisms. May made major theoretical contributions to two areas of ecology: population biology and community ecology. In the former, he created novel insights into the central question of why populations of many species fluctuate from year to year and in the latter, he challenged conventional wisdom about the causes of natural variation in the stability and resilience of ecological communities such as coral reefs, arctic tundra or tropical forests.

By the mid-1960s, long-term studies of populations of insects, birds and mammals, together with mathematical models that represented the underlying ecological processes, had revealed several key principles. First, populations are rarely completely stable in numbers from year to year, second, some populations, such as arctic small mammals, show more or less regular periodic oscillations with periodicities of several years[7], and third, yet other species appear to fluctuate wildly in numbers, leading, for instance, to unpredictable outbreaks of insect pests on agricultural crops or epidemics of disease in human populations.

These various patterns were explained by ecologists as being a result of the interaction between density-dependent and density-independent factors that influence numbers. Density-dependent factors, such as competition for food, tend to damp fluctuations because their severity in suppressing reproduction or increasing mortality, increases with population density. Density-independent factors, such as extreme weather, may cause random population crashes or booms independent of the number of individuals in the population. Regular oscillations were explained as a consequence of delayed density-dependence, in which there is a lag between an increase in population size and an increase in the mortality effect. An oft-cited example is where a predator species responds to an increase in the density of its prey by reproducing more successfully and eventually driving its prey population down, followed by a lagging decline in predator numbers.

In the 1950s and 1960s there was a major debate about the relative importance of density-dependent and density-independent limitation of populations, with the Australian ecologists Andrewartha and Birch championing the 'density-independent' school,[8] while British ecologists such as Varley and Lack emphasised density-dependence.[9]

May's seminal contribution to the theoretical debate about population fluctuations was to show that even the simplest, non-

[4] Shine (2008).

[5] May (1973).

[6] The history of the Silwood group led by Southwood, and its extraordinary influence in UK science and science policy, as well as its international pre-eminence, has been well-documented in *The Silwood Circle* (Gay (2013)).

[7] Elton (1942).

[8] Andrewartha and Birch (1954).

[9] Varley (1963). Lack (1954).

linear, deterministic population models for organisms with discrete generations (first order difference equations) could produce a wide range of behaviours, from complete stability, to damped or undamped oscillations and chaotic (apparently random, but in fact deterministic) fluctuations, depending on the strength of delayed density dependence.[10] More complex models also showed similar properties provided they included sufficiently strong delayed density dependence.

For example, a very simple model of population dynamics with discrete generations is:

$$N_{t+1} = N_t \exp[r(1 - N_t/K)]$$

Where N = population size
r = intrinsic growth rate of the population
K = 'carrying capacity'—the environmental limit on the population due to factors such as food supply or breeding sites
t = generation

This model can produce a very wide range of population trajectories, depending on the value of r as shown in Fig. 4.

As May put it: 'most existing work [by population ecologists] is based … on the assumption that if density-dependent 'signals' could be dissociated from the confounding environmental noise, the population would be regulated to a steady, constant value'.[11] In other words, May's findings re-oriented the task of population ecologists from debating the relative importance of deterministic density- and stochastic density-independent factors to understanding the range of dynamics that could arise from density-dependence on its own (Fig. 4). It is now generally accepted that both density-dependent and density-independent factors influence populations, although it has proven difficult in natural populations to distinguish between deterministic chaos arising from delayed density-dependence, and random fluctuations caused by environmental noise.

Epidemiology

In the 1970s, May spent his summers in the UK, interacting with ecologists many of whom studied consumer-resource dynamics, including the interactions between predators and their prey, as well as pathogens and their hosts. The original mathematical model of predator–prey interactions, developed in the early twentieth century by Lotka and Volterra,[12] involving a pair of coupled first-order differential equations, was neutrally stable and became unstable with the addition of most biological details. Predators tended to overexploit their prey leading to a population crash, followed by prey numbers recovering in the absence of their enemies, the result being cycles of ever-increasing amplitude until one species went extinct. This raised the question of how real resource-consumer interactions persist. May first engaged with this problem in work
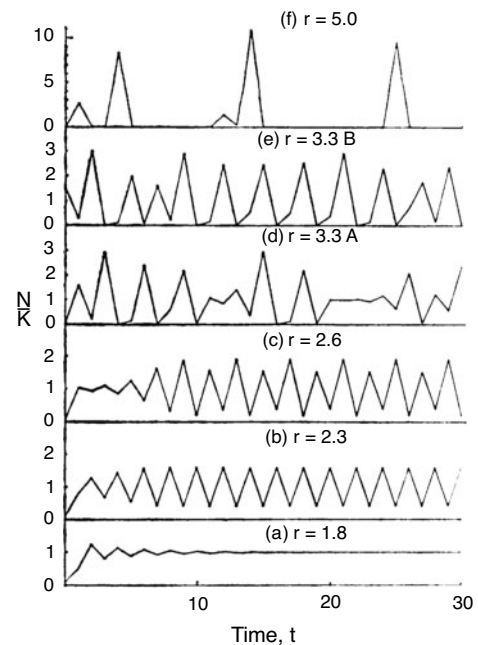

Fig. 4. From May (1974). The two cases of r = 3.3 refer to different values of N/K. Reprinted with permission from the American Association for the Advancement of Science.

with M. P. Hassell in the 1970s. They studied parasitoids—small insects (typically flies or wasps) whose larvae develop by feeding on or in the bodies of other insects which they eventually kill. Only one host is required for development and hence parasitoids are intermediate between predators and parasites/pathogens. Many pest species are hosts to parasitoids that have been used extensively in biological control. Understanding how these interactions persist was thus of practical as well as fundamental interest. In a series of papers, Hassell and May dissected the factors that might promote coexistence, concentrating on the physical and statistical refuges that allow some hosts to survive periods of high parasitoid density,[13] and latterly exploring the role of explicitly spatial processes.[14]

Interactions between pathogens and their hosts, including human hosts, are also examples of resource-consumer interactions. But the science of epidemiology had developed from a more statistical background with the role of dynamics being less appreciated (with notable exceptions such as the work of Macdonald on malaria).[15] In the mid-1970s, R. M. Anderson began to take a much more ecological approach to disease dynamics. He quickly started collaborating with May, and over the next fifteen years together they revolutionised epidemiological modelling. We write in the middle of the Covid-19 pandemic when *R* numbers and epidemiological models are discussed nightly on the news: the models used

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[10] May (1974). May (1976). May (1977).

[11] May (1974).

[12] Lotka (1925). Volterra (1926).

[13] Hassell and May (1973). Hassell and May (1974).

[14] Hassell and others (1991).

[15] Macdonald (1957).

are the direct descendants of those developed by Anderson and May.[16]

Anderson and May set out a new framework for host-pathogen dynamics.[17] They distinguished between microparasites where individuals need just to be categorised as susceptible or infected (other categories such as exposed and recovered can be added) and macroparasites, where a tally needs to be kept of the burden of infection. If you have influenza (a microparasite) the number of viral particles in your body is of less interest epidemiologically than if you have tapeworms. Anderson and May developed the rich mathematics underlying the dynamics and showed the value of concepts such as the now-famous R-number, as well as the threshold host population density below which a disease cannot spread. Understanding these processes gave insight into the average age of infection, the role of individual and herd immunity, and how optimally to deploy vaccines. The advent of the HIV epidemic highlighted the importance of sexually transmitted diseases that have very different transmission dynamics to those of diseases caused by pathogens such as influenza and tapeworms that are contracted in the environment. Their pioneering HIV models highlighted the critical importance of the transmission matrix (incorporating information on the distribution of partner numbers in both sexes and who has sex with whom), although the then UK prime minister resisted advice to try to measure it (fortunately the Wellcome Trust stepped in). Further work examined within-host disease dynamics where the interaction between the pathogen and elements of the immune system can be studied by what are essentially predator–prey models. A characteristic of the Anderson-May approach was a close link between theory and data, capitalising on the large amount of information available for human diseases.

It is often asserted that disease-causing agents, including viruses and bacteria, evolve over time to become less virulent, and thereby avoid entirely killing off their host population. This idea was first articulated in the nineteenth century by Theobald Smith as the 'law of declining virulence'. A straightforward argument from natural selection suggests this is implausible, because mutations that favour short-term gain, even if it involves killing the host, will out-compete genotypes that conserve resources for the future. But nevertheless, there are documented examples of disease agents, including the myxomatosis virus in Australia, evolving reduced pathogenicity. May and Anderson showed that in theory, whether or not this is a plausible pathway depends on the interaction between transmissibility and virulence of the parasite or pathogen.

May's and Anderson's work on human disease was summarised in their 1991 monograph.[18] Much of this 800-page book was written in a three-week period while the authors were guests of the Rockefeller Foundation at their Bellagio villa on Lake Como; time spent between intensive periods of writing in the morning and evenings punctuated by discussion over strenuous mountain hikes in the afternoon.

Community ecology

May made a major contribution to community ecology, the study of large assemblages of interacting species. His influence was both direct and indirect: he derived new theoretical results that have set a research agenda that continues today, and he continued and reinforced a transformation of the subject from organized natural history to a quantitative science.

May's most notable work in this area is on complexity and stability, and his formulation of what is sometimes called 'May's Paradox'.[19] Natural communities of plants and animals clearly persist over considerable periods of time, despite the fact that simple mathematical models of interactions between predators and prey, or other resource-consumer relationships, are often dynamically unstable. By the 1960s, ecologists had concluded that more complex communities are more stable, a belief never explicitly justified but based on the intuition that the many feedback loops present in large communities are likely to buffer external perturbations. In 1972, May's theoretical analysis showed that more complex, random, communities were, in fact, not more stable, and initiated a research programme for the subsequent decades aimed at understanding which aspects of real communities might promote stability.[20]

May's approach to the complexity-stability issue illustrates well how he tackled many questions in community ecology.[21] He first simplified the problem so that it was amenable to mathematical analysis. In this case he assumed the dynamics of a system with S species could be modelled by a set of S differential equations, and that an equilibrium existed that might or might not be stable. Linearising the system about the equilibrium, he obtained an $S \times S$ matrix, the 'community matrix', where each element represents the effect of a small change in the abundance of one species on that of another in the community. Local stability of the community is guaranteed if the real parts of all the eigenvalues of the community matrix are less than zero. May then abstracted the system further and explored the stability of randomly constructed community matrices where the non-diagonal elements of the community matrix were either zero (with probability 1-C) or picked at random from a statistical distribution with variance σ^2 (diagonal elements were assumed to be negative, reflecting intra-specific density-dependence). He then turned to cutting-edge mathematics to study the distribution of eigenvalues. In the mid-1970s, the theory of random matrices was relatively poorly developed and May used a mixture of formal maths and heuristic insight to conclude that stability requires $\sigma\sqrt{SC} < 1$. An increase in species number (S), connectivity (C) or variance in interaction strength (σ^2) all make stability less likely—a result that surprised everyone, hence May's Paradox.[22]

As May was well aware, real communities do not have random community matrices and in his ground-breaking monograph he explored various constraints on the community matrix and the

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[16] Anderson and May (1985).

[17] Anderson and May (1979). May and Anderson (1979). May and Anderson (1983). May and Anderson (1987). Anderson and May (1991).

[18] Anderson and May (1991).

[19] May (1973).

[20] May (1972).

[21] May (1972). May (1973).

[22] For a modern rederivation and extension of May's results using maths developed in the last 15 years see Allesina and Tang (2015).

possibility that communities may be compartmentalised into weakly connected modules.[23] Later ecologists have explored many other possibilities. A limitation of May's approach is that it assumes a community has a potentially stable equilibrium, and that it does not say whether the consequence of instability is the loss of one species or cascading extinctions and a much more substantial collapse. Again, recent work has illuminated these questions, though extending May's work to the general non-equilibrium case is an outstanding challenge.

Much research in community ecology has focussed on understanding the mechanisms in natural communities that result in greater complexity leading to greater stability. Foremost among the experimental work in this field is that of Tilman and his students on grassland communities.[24] This work has shown how, in more complex communities, resources are partitioned among species and how this leads to greater resilience in the face of environmental change.

May made other important contributions to community ecology. Some of his earliest work, in part with Robert MacArthur, concerned limiting similarity.[25] Suppose you have a spectrum of seeds of different size; how many species of bird might coexist along this 'niche axis', specialising on a certain seed size interval? May derived theoretical limits to how similar species might be and hence the number that can coexist. However, his hope that these rules might be generalisable to arbitrary resource distributions was not borne out. Other ecologists, often using approaches he pioneered, showed that limiting similarity and the number of species that can coexist on a resource is very sensitive to the specific biology of the system.

Conservation and taxonomy

It often amazes non-ecologists how poor an estimate we have of the number of species on earth, even relatively large species such as insects, let alone microorganisms. It certainly amazed May, who wrote several papers on this topic in the 1980s and 1990s.[26] In 2011, he wrote: 'It is a remarkable testament to humanity's narcissism that we know the number of books in the US Library of Congress on 1 February 2011 was 22,194,656 but cannot tell you—to within an order-of-magnitude—how many distinct species of plants and animals we share our world with'.[27] May's work in this area differs from his other work on community ecology in that it did not involve sophisticated modelling but a razor-sharp summary and analysis of the available evidence, as well as a clear statement of where further study may be most productive and a heartfelt lamentation about the number of species that will go extinct before their enumeration. Together with several co-authors, he estimated that current rates of extinction of species is several orders-of-magnitude higher than the average for the fossil record.[28] He also wrote an elegant summary and extension of how conservationists might best balance competing demands when deciding which taxa to prioritise in decisions about conservation. Is rarity more important, or is taxonomic distinctiveness?[29] And if the latter, how is it to be characterised, at the level of species, family, order and so on? More recently, these ideas have been encapsulated in the Zoological Society of London's EDGE of Existence programme, a conservation initiative that focusses on 'evolutionarily distinct and globally endangered species'.

Dispersal

Together with Hugh Comins and William D. Hamilton, May analysed the conditions under which dispersal is favoured by natural selection.[30] Most organisms disperse from their birthplace, in spite of the fact that this incurs the disadvantage of leaving a known favourable habitat for the unknown and thus facing the risk of mortality during dispersal. In their modelling, they identify the factors that favour dispersal, including the probabilities of colonising empty sites, of sites becoming extinct, and the frequency of genes *for* dispersal.

The banking system

May's work on complex networks in ecology and epidemiology gave him a unique perspective on the fragility of the global banking system during and after the 2008 financial crisis. He developed a series of what he called 'toy models' of the banking system where banks were viewed as nodes in a network, each with certain assets and liabilities. A fraction of assets were loans to other banks and a fraction of liabilities borrowings from other banks, and the collapse of one bank might cause cascading collapses through this network of mutual obligations.

In an influential 2011 'Perspective', May teamed up with Andy Haldane, the chief economist at the Bank of England, to draw lessons from this approach for prudential regulation.[31] Traditionally, mandating capital and liquid asset requirements has been the main tool of regulators, but their levels had been set to avoid the risk of individual bank failure, and these may be different to those required to avoid system failure. May and Haldane drew a parallel between highly connected large banks (those 'too big to fail') and 'superspreaders' in epidemiology, and suggested these may need greater asset reserves or other attention from regulators.

The conclusions that diversity and modularity in ecological networks are stabilising suggest interventions that might stabilise financial networks, including the segregation of retail and 'casino' banking that the industry so resists.[32] Finally, May and Haldane explored how the centralising of trading in financial derivatives on exchanges or equivalents might change the structure of a network from a cat's cradle to a hub-and-spoke configuration, so increasing

[23] May (1973).
[24] Tilman (1982).
[25] May and MacArthur (1972).
[26] May (1988).
[27] May (2011).
[28] Smith and others (1993). Tilman and others (1994).
[29] May (1990).
[30] Hamilton and May (1977). Comins and others (1980).
[31] Haldane and May (2011).
[32] May and others (2008).

system stability. This remarkable example of discipline hopping has helped the development of the new approach of macro-prudential policy making.

Government Chief Scientific Advisor

In 1995, Bob May was approached, as he himself said, 'gobsmackingly out of the blue' by the head-hunting firm Saxton Bamfylde about the job of Government Chief Scientific Advisor (GCSA). At the time, May had little experience of the science-policy interface or of the UK civil service. Nevertheless, he had three qualities that made him singularly suited to the role: his formidable intellect and ability to resolve any complex problem into its essential simplicities, his deft turn of phrase and facility expressing ideas in comprehensible ways to non-experts, and his willingness to speak truth to power without fear or hesitation, sometimes using his Australian background as a reason for choosing blunt terms that might be more difficult for a native British person to use. He also said that he drew on his experience as a schoolboy competitive debater, when he would be given the topic ten minutes before the debate and a flip of a coin determined whether he was speaking for or against the motion.

May's appointment as GCSA coincided with a major change in the job. The role had existed since the 1960s with Sir Zolly (later Lord) Zuckerman, who had advised the government during World War 2, as the first holder. Zuckerman's successors were generally not well-known public figures, following Churchill's dictum that 'scientists should be on tap but not on top', and the GCSA was supported by a small staff.

May's immediate predecessor, Sir William Stewart, had been much involved in the preparation of the white paper 'Realising our potential' that heralded the reorganisation of the research councils and the creation of the Office for Science and Technology (OST). The OST was relatively well staffed and May was its first head. The advisory board to the research councils (ABRC) that had recommended budget allocations to the individual research councils, was abolished and replaced by a new role within OST, Director General of Research Councils, with Sir John Cadogan as its first holder. Together, he and May made a formidable pair as advocates for science in Whitehall.

It is not an exaggeration to say that May transformed the role of the GCSA from a back-room boy (all previous GCSAs had been male) to a high-profile public figure, appearing frequently in the media and commenting on current science-policy matters. For instance, when the Royal Society for the Protection of Birds (RSPB) publicised an inaccurate and potentially alarming interpretation of field trials of genetically modified (GM) crops, May decided to cancel a planned walking holiday in the Cinque Terra, Italy, due to start the following day, in order to be on the BBC's Today Programme to refute the RSPB comments. He never forgave the RSPB!

In a note for Prime Minister Tony Blair, May summarised the heated, and usually confused, debate about GM crops during the late 1990s as the 'three worries'—the worry about food safety, the worry about environmental safety, and the worry about the intensification of agriculture and the role of big business. His conclusion on each of these worries was characteristically incisive. GM food and environmental safety should be assessed on a case by case basis. No-one had identified any food safety risks; environmental safety was a

potentially a more serious worry, but was carefully regulated; and intensification of agriculture was about hard choices, irrespective of whether it involves GM. You could not feed today's world population with yesterday's agriculture, but the more we take from the land, the less there is for the rest of nature.

During May's time as GCSA, he frequently commented publicly in the broadcast and print media on other high profile and urgent issues, such as Bovine Spongiform Encephalopathy (BSE, or 'mad cow disease'), climate change, and the Human Genome Project. In the last of these, during the race to the finishing line between Craig Venter and publicly funded groups along with the Sanger Centre, he played a part in negotiating the agreement with the US government to ensure that the human genome would remain public intellectual property. May recounted later that Craig Venter had said that as a result of May's success in this initiative, he, Venter, had lost a fortune: when US President Clinton announced that the human genome could not be patented, shares in Venter's company, Celera, plummeted.

Less well known, but equally critical for the affected people, was May's advice on the response to the eruption of Soufriere Hills volcano on Montserrat, a British Overseas Territory in the Leeward Islands. When, in summer 1995, the volcano became active, May was asked to advise on whether or not the whole population of the island should be evacuated. He sought advice from the top academic vulcanologists, and concluded that the capital, Plymouth, should be evacuated, but that the northern part of the island was safe for people to stay. This advice was followed and the southern exclusion zone still remains in place, Plymouth having been destroyed in a pyroclastic flow.

In addition to his recasting of the role of GCSA as a public figure, May left two further important legacies: the *Chief Scientific Advisor's Guidelines for Scientific Advice and Policy Making*, and his comparative analysis of the competitiveness of UK science. The guidelines, described by May as 'the most important thing I did' set out three principles for providing scientific advice to Government: fully acknowledge uncertainties (sometimes the answer is 'we don't know'); seek a wide range of views (it is rare that the scientific and other communities totally agree on the evidence); be totally transparent about the process and outcome of advice. These principles are simple, but as salient today as when they were first published. May lamented the fact that in successive revisions of the guidelines they became progressively more complex and bureaucratic, losing the directness and simplicity of his version.

The analysis of 'bangs per buck' of UK science in comparison with other countries was typical of May's analytical mind and clarity of thought. The work he commissioned looked at outputs such as refereed papers, citations and major prizes, expressed in relation to investment in scientific research. This became a powerful tool for influencing government ministers both in showing the extraordinary value for money of investment in UK science and in arguing for increased investment. Successive science ministers in the subsequent decades have the quoted numbers as a stock part of their speeches: with 2% of the world's population and 5% of the world's scientists, the UK publishes over 10% of the most highly cited papers, even though the UK's investment in research and development lags behind other major scientific nations. No other medium-sized or large country achieves as many bangs per buck. May also considered why the UK does so well. He pointed to one possible factor, namely

Fig. 5. Sir Timothy Berners-Lee (L) shakes hands with Lord Robert May of Oxford (R) across a table upon which rests the Royal Society's mace. Photographed at the Royal Society, on the occasion of Berners-Lee's admission as a Fellow in 2001. Photograph by Prudence Cuming Associates © The Royal Society.

that much research is done in universities, where students ferment new ideas, rather than in separate research institutes.

May was also characteristically direct in his assessment of the civil service, describing it as a suitable subject for anthropological study. One of his frustrations was that civil servants often accidentally or deliberately conflated process and outcome and were able to craft beautifully prepared documents and reports on the former as a substitute for achieving the latter.

In commenting on scientific advice as input to policy, he distinguished between what he called routine advice on well-researched problems, that could be provided by 'reagent grade scientists', and advice on really hard, novel, as yet unstudied, scientific problems, such as BSE, or AIDS in Africa, which he described as 'the clean rock'. Advice on the clean rock problems required leadership and innovation in the relevant field that could not be delivered by standard, reagent grade, scientists. May himself was, of course, a clean rock scientist in mathematical epidemiology and ecology.

Twenty years on, one can see that the change in the character of the job of GCSA has lasted: all four of his successors (each, like May, a Fellow of the Royal Society) has been the public faces of scientific advice and all have been prominent in presenting the science that supports their policy advice during crises: Sir David King during the Foot and Mouth crisis of 2001; Sir John Beddington during the Icelandic Volcano (Eyjafjallajökull) eruption of 2010 and the Fukushima Nuclear Accident in 2011; Sir Mark Walport during the winter floods of 2015; and Sir Patrick Vallance in the Covid-19 pandemic.

President of the Royal Society

When May was elected president of the Royal Society in 2000 (Fig. 5) he was unique among twentieth-century presidents in having held a major public office in addition to being a scientist of remarkable distinction. Since 1915, all presidents had been Nobel Laureates with the exception of mathematician Sir Michael Atiyah, who was a Fields Medallist, the mathematics equivalent of the Nobel (Fig. 6). May, too, worked in fields for which there is no Nobel Prize, but he had been awarded two other prizes of comparable distinction, the Crafoord and the Balzan.[33] A full list of May's

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[33] The Crafoord Prize, established by Swedish industrialist Holger Crafoord and his wife Anne-Greta is awarded in partnership with the Royal Swedish Academy, year by year successively in the fields of astronomy and mathematics; geosciences; bioscience with particular emphasis on ecology; and polyarthritis. Four Balzan Prizes are awarded each year, drawing on funds invested by Eugenio Balzan and administered by a committee of prominent European scientists.

Fig. 6. Presidents of the Royal Society—from left to right, Sir Robert May, Sir Aaron Klug, Sir Michael Atiyah, Sir George Porter and Sir Andrew Huxley. Photograph © The Royal Society.

honours and memberships is contained in the Supplementary Material accompanying this memoir.

May said that when he was elected president he did not have a list of goals in mind. However, he did bring about change, and by his own assessment he was more hands-on than his predecessors. His achievements as president can be grouped under three headings: fellowship, policy, and international.

In order to try to broaden the base from which fellows are elected, he started writing to vice chancellors to seek suggestions for potential candidates for the fellowship who might be lurking in less familiar universities. He aimed to rebalance the election of foreign members away from 'people's elderly American friends'. He also championed the election of women scientists, without sacrificing merit, and greater geographical diversity, outside the golden triangle. Shortly before May became president, the society's biological secretary, Sir Patrick Bateson, had proposed that the number of signatures needed to support a candidate for election should be reduced from six to two. May thought that this was 'a really bad idea' but he concluded that the proposal was too far down the track for him, as incoming president, to stop it, in spite of the fact that he thought it would tip the scales too far towards cronyism and cliques.

He successfully engaged the society in supplying independent advice and comment to government on science and policy matters. Prior to May's presidency, the Royal Society had seen itself as a scientist's club and it thought of the scientific community as its primary audience. As May himself put it 'it was mainly an organisation for electing people and writing their obituaries'.

Shortly before May became president, the Royal Society began to dip its toe into the science and policy world, by publishing an independent assessment of the paper published by Arpad Pusztai that falsely claimed to show GM potatoes poison rats. However, this was at the request of Science Minister (Lord) David Sainsbury rather than a spontaneous initiative of the Royal Society, and, according to May, was 'more or less against the instincts of Aaron [then-president Klug]'. The first draft of the report was, as May put it 'so obscurantist and equivocal and convoluted that it's impossible for the lay reader to decide whether you're saying the work is sound or unsound'. May urged a re-write, and the final version said that Pusztai's study was so flawed in design, execution and analysis that no conclusions could be drawn from it. This was a formative experience for the Royal Society in engaging in a public controversy about a high-profile scientific issue.

May was more proactive in engaging with government policy than his predecessors, without sacrificing the society's independence. An important product of this was the Follett Report into the handling of the 2001 Foot and Mouth Disease epidemic. Unlike the Phillips Enquiry into BSE, the Follett report was produced quickly and at modest cost. Nevertheless, its recommendations on how to handle a future epidemic, especially in relation to vaccination, were accepted by the government. Importantly, Follett discussed his

Fig. 7. For forty-one years between 1974 and 2016, Bob organised an annual summer walk with his colleagues. Left: Judith, Bob, John Krebs and Charles Godfray. Right: Bob, Charles Godfray and Mike Hassell. (Photographs courtesy of the authors.)

emerging conclusions with the European Commission (EU), as the rules on international trade and vaccination were determined by the EU. May, along with others including Sir John Beddington, Lord Stern and Baroness Blackstone, also successfully challenged the policy of Clare Short, Secretary of State for International Development, when she proposed to cut the budget for tertiary education and research in developing countries, and channel it instead into primary education.

The Royal Society has always had a strong international programme, and during May's presidency, he supported the creation of a new body, the European Academies Science Advisory Council (EASAC) to act as a voice for national academies across Europe. It was also during May's presidency, in 2005, that the Group of Eight (G-8) statement on climate change, supported by the national academies of the intergovernmental (G-8) was produced, although May said that he was not directly involved in drafting the statement.

House of Lords

In 2001, May was appointed to the House of Lords (as Lord Robert May of Oxford), the second chamber of the UK parliament, as an independent 'cross-bencher' (that is, not a party-political appointment) under a new initiative of the Blair government to create so-called 'people's peers'. During his time in the Lords, he served on two select committees, the Science and Technology and Economic Affairs. One of us (JK) chaired the Science and Technology Select Committee while May served as a member, and was able to observe at first hand his forensic and sharp interrogation of witnesses, including government ministers. Although May was a fluent and skilful debater, he was occasionally frustrated by the formal and stilted style of debate in the Lords and sometimes he made his most important contributions in meetings with ministers outside the chamber, and in this way was able to help to improve legislation.

Social and sporting life

May loved the social side of his academic life, and this was often focussed on sporting competitions and other physical activities. At Princeton in 1974, May overheard two graduate students in the Ecology and Evolutionary Biology Group talking about running to keep fit. He challenged the students to a mile run in the Princeton University stadium. May won the race in six minutes twelve

seconds. The race, that came to be known as the Eno Mile (named after the building in which the group worked), became an annual event, and May regularly finished in under six minutes. After moving to Oxford in 1988, he ran regularly with John Krebs, covering more than 15,000 km over a twenty-five-year period. May was a keen table tennis player and even had a table tennis table in his dining room at Princeton instead of a dining table. As with all games (he played five-a-side football, tennis and croquet—and even decided the order of authorship of one of his papers by a croquet contest), May was always fiercely competitive, very focussed on doing his best and, if possible, winning. It was said of May that when he came home in the evening and played with his dog (a much-loved poodle named Perri), he played to win.

May was a loyal colleague and friend. For forty-one years between 1974 and 2016, he organised an annual summer walk with colleagues. In the early years, the walks were in Britain, but in later decades they were in the Austrian, French Italian, Swiss and Slovenian Alps, Pyrenees and the Picos de Europas (Fig. 7). In addition to the core group of participants (including the three authors of this memoir) colleagues who had worked with May and/or were deemed to be suitable walking companions joined the group with varying frequencies. These walks, combining physical and intellectual exercise with natural history and gossip, produced many memorable stories, retold many times in hotel bars before and after supper. His wife Judith was a regular participant in the summer walks and helped to keep a meticulous record of each year's trip. In some of the early years, Bob's and Judith's daughter Nome, a talented jewellery-maker now living in Oregon, USA, also came on the walks.

Appraisal

May was without doubt one of the most brilliant, versatile and energetic scientific minds of his generation. Although not known for a single discovery (he said he had a short attention span), in each of the scientific areas that he touched, he was able to reduce complex problems to their essential simplicities. A complete bibliography of his published work may be found in the Supplementary Material accompanying this memoir. His theoretical work caused ecologists to reconsider some of their basic assumptions and spawned several new research agendas, in particular among population and community ecologists. In his work on infection disease

epidemiology with Anderson, he reduced a complex problem to few key variables, notably the R-number or basic reproduction number, that entered the public lexicon during the coronavirus pandemic. His immense intellectual contribution was recognised by many major awards and prizes. Had there been a Nobel Prize for ecology, May would undoubtedly have won it.

May was unique among scientists in the UK of his generation in combining two careers in one life: the outstanding researcher in his chosen field of ecology and a major figure in the public sphere as government chief scientific advisor and trenchant commentator in broadcast as well as print media. He also played a full role as a citizen of the scientific community on numerous trustee boards, committees and so on. On top of this he served with distinction as president of the Royal Society.

Conflicts of interest

Acknowledgements

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