RETROSPECTIVE

Alison Galvani^a, Alan Hastings^b, Simon A. Levin^{c,1}, and Burton H. Singer^{d,e,f}

Robert (Bob) May, Baron May of Oxford, a long-time International Member of the National Academy of Sciences, passed away on April 28, 2020, in Oxford, United Kingdom, from "frailties of old age, Alzheimer's disease, and pneumonia," at the age of 84. He is survived by his wife Judith, his daughter Nome, and legions of students and colleagues. Across six decades, Bob had a transformative impact on myriad fields: mathematical biology, ecology, epidemiology, public policy, and finance. His intellect, sense of loyalty to colleagues and students, and commitment to humanity made him a towering giant in science and science policy.

Bob May was born in Sydney, Australia, where his talents as a mathematician were evident from an early age. Bob was trained in theoretical physics at the University of Sydney by the distinguished physicist Robbie Schafroth, receiving his PhD at 24 years old for his work on bosons and superconductivity. Nonetheless, May traced his good luck in mentorships back to his high school chemistry teacher Lenny Basser and was always quick to give accolades to the many influences on his development, from teachers and colleagues alike. For those who knew him, it was clear that he made it a point to pay forward this debt through his investment in his own students and others.

After a postdoctoral stint with Max Krook at Harvard University—during which he met his future wife, Judith—Bob accepted a faculty position at the University of Sydney, and within a few years had risen to one of the first "Personal Professorships" at the university. In his early work, he focused on problems in plasma physics and related fields and quickly rose to prominence. However, soon after, concerned for the fate of the planet and feeling he had a larger debt to society, he turned to applying the mathematical techniques he had mastered during his graduate studies to explore the stability and complexity of ecological systems, helping to lay the foundation of modern theoretical ecology. After meeting the pioneering theoretical ecologist Robert MacArthur while spending a sabbatical at the Institute for Advanced Study in Princeton, in 1973, May accepted an endowed professorship at Princeton University as the replacement for MacArthur after the latter's death. MacArthur knew that he was dying and suggested that Princeton hire May. Although May initially declined, Judith urged him to reconsider. Bob was convinced and called the then department chair, the late John Tyler Bonner, who confirmed



Robert M. May, c. 2004. Image credit: Royal Society/Laurence Bulaitis.

that the offer still stood. The Mays spent many happy and productive years in Princeton, transforming the ecology group. In 1988, faced with a new challenge, May moved to the United Kingdom to a special professorship affiliated both with Oxford University and Imperial College, and remained there for the rest of his life.

May's early contributions to ecology were seminal, creating unique perspectives and hypotheses concerning what makes systems robust and stable, limits to diversity, and the potential for critical transitions, all topics that remain at the core of the subject. He wrote prolifically and also advanced the field through his coeditorship with the late Henry S. Horn of the influential *Princeton Monographs in Population Biology*, in which he benefited greatly from the wisdom and skills of the in-house Princeton University Press editor, his wife Judith.

The centrality of May's contributions to ecology was confirmed in his influential 1973 Princeton monograph, *Stability and Complexity in Model Ecosystems* (1). One of the central issues in ecology is the explanation of the distribution and abundance of species,

^aCenter for Infectious Disease Modeling and Analysis, Yale School of Medicine, New Haven, CT 06510; ^bDepartment of Environmental Science and Policy, University of California, Davis, CA 95616; ^cDepartment of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544; ^dEmerging Pathogens Institute, University of Florida, Gainesville, FL 32611; ^eDepartment of Mathematics, University of Florida, Gainesville, FL 32611; and ^fWeill Cornell Medicine, Graduate School of Medical Sciences, Cornell University, New York, NY 10065

Author contributions: A.G., A.H., S.A.L., and B.H.S. wrote the paper.

The authors declare no competing interest.

ww.pnas.org/cgi/doi/10.1073/pnas.2016616117

Published under the PNAS license.

¹To whom correspondence may be addressed. Email: slevin@princeton.edu.

First published September 10, 2020.

and this monograph and the research publications that led to it brought new perspectives to this issue and set the stage for a continually expanding research agenda that is still relevant today. Beginning with the classic work of one of the founders of ecology, Charles Elton, prominent dogma in ecology was that larger, more complex systems should be more stable. By emphasizing stability as a key concept and showing that theoretical support was lacking for increasing stability of complex systems, May's work set ecologists on the path of finding alternative explanations for the presence of highly diverse and robust natural systems. May himself used the approach developed in this monograph in many insightful ways, from ecology to banking.

Shortly after his monograph appeared, May published a series of highly original papers (2-4) on simple ecological models that were not stable, but in fact exhibited what is now called chaotic dynamics. May presented his findings in 1974 at a lecture at the University of Maryland (with one of us, S.A.L., in attendance as witness), where it found resonance with the work of the University of Maryland mathematician James Yorke, also in the audience, who, with his student Tien-Yien Li, coined the term "chaos" (5). In their own seminal paper, Li and Yorke (5) acknowledged this fortuitous interaction: "Added in proof: May has recently discovered other strong properties of these maps in his independent study of how the behavior changes as a parameter is varied." This inverted the usual paradigm of ecology drawing lessons from mathematics by showing that analysis of the dynamics of simple ecological models had importance for other disciplines as well. These papers showed that, even in some very simple models, the accepted idea that the main source of ecological unpredictability was exogenous stochastic factors failed. This perhaps fundamental lack of predictability in ecology once again established whole research directions. May's unique influence went beyond his fundamental discoveries, being enhanced by his ability to simply and clearly explain complex ideas.

May, primarily in collaboration with British biologist Michael Hassell, developed deep new understanding of another long-standing central question in ecology, the nature of interactions between hosts and parasitoids (6). Roughly 15 to 20% of all insect species are parasitoids, insects that reproduce by laying their eggs in a developing stage of another insect, the host. Additionally, parasitoids play a vital role in controlling the populations of insects that are crop pests or have other negative impacts. The classic model of hosts and parasitoids was developed in the 1930s by Nicholson and Bailey, who showed that parasitoids could reduce the growth rate of host populations, but that the interaction invariably led to unstable dynamics with cycles of increasing magnitude. Hassell and May wondered how these interactions were stabilized in nature and explicated those factors in a series of brilliant papers, summarized in Hassell's monograph in the Princeton series (7).

The work on hosts and their exploiters transitioned into one of the most important contributions of

mathematics to biology. In a fortunate occurrence for science and the world, Bob met and began interacting with the brilliant young scientist Roy Anderson; together, they created a major scientific transition by viewing the epidemiological dynamics of infectious diseases through the lens of processes encompassing ecology of (other) biological populations. While much work in ecology is aimed at maintaining biodiversity by promoting species persistence in ecological systems, pest species and invasive species in general are targets for extinction; similarly, a goal in the management of infectious diseases is to suppress disease incidence by driving pathogens to extinction. The mathematical formulation by May and Anderson of these insights and their prolific work developing and applying mathematical models for diverse epidemiological situations catalyzed the field of epidemiological modeling to a level that is today applied to every infectious disease. The breadth of the public health challenges to which they applied these approaches remains unparalleled, and their textbook (8) is the gold standard in the field. Their breakthrough advances spurred national and international improvements in public health policy, improvements that saved countless lives globally, and are at the basis of almost all of the models being used during the current pandemic.

May's seminal use of models to inform conservation and public health policies led to his appointment as Chief Scientific Advisor to the UK Government and appointment to the Presidency of the Royal Society, the prestigious society of which Isaac Newton was once the president. Bob's public service was honored by knighthood in 1996, by membership in the House of Lords, and by the award of the Order of Merit in 2002. Robert May's scientific and leadership contributions were also recognized by several honorary doctorates, including from Princeton and Yale, as well as with regular or foreign memberships in the Royal Society, the Australian Academy of Science, the US National Academy of Sciences, and the Academia Europaea. His scores of awards included the Blue Planet Prize, the Crafoord Prize, and the Balzan Prize.

Bob inspired many generations of scientists and was an unwavering advocate for women in science. While serving in the demanding roles of Chief Scientific Advisor and then President of the Royal Society, Bob nonetheless accepted and supervised one of us as a PhD student. Despite the incredible professional demands on his time from his day jobs, Bob was extraordinary even among the extraordinary. He had afternoon tea with his student (A.G.) twice a week, during which she was enthralled by his sharp-witted anecdotes that sometimes included tales of Queen Elizabeth, political figures, and renowned scientistsand at other times featured his beloved poodle Perri. Bob's ever-present veneer of playful competitiveness belied his empathy and generosity. Bob valued his time but also gave it generously to students and colleagues. He taught them both how to do rigorous science and also how to play croquet and other games, including ping-pong and real tennis (originally "royal tennis," with

a special indoor court and rules dating from the time of Henry VIII and earlier).

Leading up to and following the global financial crisis of 2008, Bob again transcended the silos of traditional disciplines in his application of ecological principles to evaluate the systemic risk in banking "ecosystems" and to inform protective regulations over banking systems. This began with a joint publication with one of us and his former student George Sugihara (9), warning of the dangers of systemic risk in the banking system, but as with any subject in which May dipped his toe, he did not stop there after the warnings of that paper were borne out. He began an intense collaboration with his student Nimalan Arinaminpathy (10) and Andy Haldane of the Bank of England, which resulted in remarkable insights regarding regulations that would produce more stable financial markets (11).

Robert May left his mark on science and policy in a multitude of ways. His own scientific contributions helped to shape aspects of physics, ecology, the epidemiology of infectious diseases (including his work on HIV-AIDS with Anderson and modern efforts to deal with COVID-19), and financial regulation. Beyond that, he created a model for how science can inform policy through his own service and by helping to attract brilliant colleagues in the United Kingdom into such service. He was a wonderful spokesman for science because of his brilliant ability to communicate through his lectures and writings (including regular "News and Views" in Nature). His leadership is sorely missed in the current times. Perhaps above all, he was a citizen of the world, a loyal and supportive mentor and colleague, and a model for how science can serve humanity. In this way, as in many other ways, Bob's enduring legacy will continue.

- 1 R. M. May, Stability and Complexity in Model Ecosystems (Princeton University Press, 1973).
- 2 R. M. May, Biological populations with nonoverlapping generations: Stable points, stable cycles, and chaos. Science 186, 645–647 (1974).
- 3 R. M. May, Biological populations obeying difference equations: Stable points, stable cycles, and chaos. J. Theor. Biol. 51, 511–524 (1975).
- 4 R. M. May, Simple mathematical models with very complicated dynamics. Nature 261, 459–467 (1976).
- 5 T.-Y. Li, J. A. Yorke, Period three implies chaos. Am. Math. Mon. 82, 985–992 (1975).
- 6 M. P. Hassell, R. M. May, Stability in insect host-parasite models. J. Anim. Ecol. 42, 693–726 (1973).
- 7 M. P. Hassell, The Dynamics of Arthropod Predator-Prey Systems (Princeton University Press, 1978).
- 8 R. M. Anderson, R. M. May, Infectious Diseases of Humans: Dynamics and Control (Oxford University Press, 1991).
- 9 R. M. May, S. A. Levin, G. Sugihara, Complex systems: Ecology for bankers. Nature 451, 893–895 (2008).
- 10 R. M. May, N. Arinaminpathy, Systemic risk: The dynamics of model banking systems. J. R. Soc. Interface 7, 823–838 (2010).
- 11 A. G. Haldane, R. M. May, Systemic risk in banking ecosystems. Nature 469, 351–355 (2011).

