

May R M. *Stability and complexity in model ecosystems*. Princeton, NJ: Princeton University Press, 1973. 235 p.  
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This book aims to gain general ecological insights by studying mathematical models. A variety of theoretical models are used in pursuit of this aim, linked together by their all bearing on aspects of population stability in biological communities of interacting species. [The *SCI*® and *SSCI*® indicate that this book has been cited in over 905 publications.]

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September 29, 1988

In 1970-1971 I was professor of theoretical physics at the University of Sydney and a founding member of the Society for Social Responsibility in Science, in Australia. In the course of educating myself about environmental issues, I read Ken Watt's book *Ecology and Resource Management*.<sup>1</sup> This book sets out clearly the arguments underpinning what at that time was the conventional wisdom that complex ecosystems are more stable (in the sense that they are better able to handle natural or human disturbances). One of these arguments was that simple mathematical models for one predator/one prey systems are unstable, in the sense that linearised analyses can often exhibit diverging oscillations (nonlinear limit cycles, much less "chaos," were not yet recognised in the ecological literature). The same evening that I read this, I made the calculations showing that the corresponding simple models for  $n$  predator/ $n$  prey systems are typically even less stable. Charles Birch, a noted ecologist at the University of Sydney, encouraged me to write this work up and also put me in touch with Southwood, Maynard Smith, Robert H. MacArthur, and other ecologists during my sabbatical leave at Oxford and the Institute for Advanced Study at Princeton, in 1971-1972.

Largely owing to MacArthur, ecologists at that time had begun to formulate many questions in mathematical form.<sup>2</sup> I happened to have the right skills at the right time, and a range of topics opened up: the stability of various kinds of randomly assembled food webs, limit cycles in predator/prey associations, the limits to similarity among coexisting competitors, the dynamics of mutualistic associations, the influence of demographic and environmental stochasticity upon all these phenomena (which

can often make for qualitatively different conclusions), and many other things. Returning to Sydney, I pulled all this work together over the Australian winter of 1972, producing the monograph that MacArthur (who at that time was dying from cancer) had asked me to write. Around this time it became increasingly clear that the work was no longer a part-time diversion, and I phoned Princeton to ask if the position I had declined earlier in the year was still open. It was, and I moved to the Department of Biology at Princeton University in February 1973. The book itself sold quickly, and I added new material for the second edition that appeared in 1974.

Some of the broader themes are the relation between stability and complexity in general multispecies models; the relation between stability in randomly fluctuating environments as opposed to deterministic ones; and the way environmental fluctuations are liable to put a limit on niche overlap, a limit to similarity, among competing species in the real world. Minor themes include the way nonlinearities can produce stable limit cycle oscillations in real ecosystems; the role played by time delays in feedback mechanisms, and the way that addition of extra trophic levels can stabilise them; the relation between stability within one trophic level and total web stability; and why strong predator-prey links may be more common in nature than strong mutualistic links. The book is primarily directed at the field and laboratory ecologist, and the text is aimed to be accessible to people with minimum mathematical training (with technicalities relegated to appendices).

I think it is fair to say the book has been influential in overturning the simple notion that complex ecosystems are more stable, leading to a continuing search for the kinds of special relations and structure that make for robustness in the face of unpredictable environmental variability.<sup>3</sup> It may even be that tropical ecosystems are so much richer largely because their environment is more predictable than that of temperate and boreal places. The book also contributed to a still-unfolding understanding of the dynamical behaviour that can arise from nonlinear interactions among species,<sup>4</sup> much of this understanding (the occurrence of cycles, and so on) is now sufficiently a part of the subject that it is taken for granted, sometimes, paradoxically, by those who are at the same time critical of mathematical models in ecology. In some areas the book is now seriously dated (especially the work on niche overlap and limits to similarity among competitors), but I think many of the questions it raises are still open—which may be why the book is still cited.

1. Watt K E F. *Ecology and resource management: a quantitative approach*. New York: McGraw-Hill, 1968. 450 p. (Cited 260 times.)

2. MacArthur R H. *Geographical ecology: patterns in the distribution of species*. New York: Harper & Row, 1972. 269 p. (Cited 1,275 times.)

3. Pimm S L. *Food webs*. London: Chapman and Hall, 1982. 219 p. (Cited 70 times.)

4. Begon M, Harper J L & Townsend C R. *Ecology: individuals, populations, and communities*. Sunderland, MA: Sinauer, 1986. 876 p.