CHAPTER 1

Introduction

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In this introductory chapter, we indicate the aims and structure of this book. We also indicate some of the ways in which the book is not synoptic in its coverage, but rather offers an interlinked account of some major developments in our understanding of the dynamics of ecological systems, from populations to communities, along with practical applications to important problems.

Ecology is a young science. The word ecology itself was coined not much more than 100 years ago, and the oldest professional society, the British Ecological Society, is less than a century old. Arguably the first published work on ecology was Gilbert White's *The Natural History of Selborne*. This book, published in 1789, was ahead of its time in seeing plants and animals not as individual objects of wonder—things to be assembled in a cabinet of curiosities—but as parts of a community of living organisms, interacting with the environment, other organisms, and humans. The book has not merely remained in print, but has run steadily through well over 200 editions and translations, to attain the status of the fourth most published book (in the sense of separate editions) in the English language. The following excerpt captures White's blend of detailed observation and concern for basic questions.

> Among the many singularities attending those amusing birds, the swifts, I am now confirmed in the opinion that we have every year the same number of pairs invariably; at least, the result of my inquiry has been exactly the same for a long time past. The swallows and martins are so numerous, and so widely distributed over the village, that it is hardly possible to recount them; while the swifts, though they do not all build in the church, yet so frequently haunt it, and play and rendezvous round it, that they are easily enumerated. The number that I constantly find are eight pairs, about half of which reside in the church, and the rest in some of the lowest and meanest thatched cottages. Now, as these eight pairs—allowance being made for accidents—breed yearly eight pairs more, what becomes annually of this increase? and what determines every spring, which pairs shall visit us, and re-occupy their ancient haunts?

This passage is unusual in giving quantitative information about the population of swifts in Selborne two centuries ago, a small exception to the almost universal absence of population records going back more than a few decades. It is even more remarkable for its clear articulation of the central question of population biology: what regulates populations? Interestingly, the swift population of Selborne these days is steadily around 12 pairs, which in ecological terms is not much different from eight, even though much of their environment has changed—entries to the church tower all wired-off to keep out squirrels, and the gentrified cottages no longer low and mean with their thatch, when it remains, neatly wired down (Lawton and May, 1983). Interpreted generously, these population data on Selborne's swifts could be seen as one of ecology's longest time series, so it is sobering to realize there is still no agreed explanation of what actually regulates the swifts' numbers.

Moving on from Gilbert White, the first half of the twentieth century saw some more explicitly mathematical models aimed at understanding the dynamical behaviour of populations. Notable examples include Ross' work on malaria, with its first introduction of the basic reproductive number, R_0, discussed in later chapters of this book, and Lotka and Volterra's indication of the inherently oscillatory properties of prey–predator systems. Despite this, ecology seems to us to have remained a largely observational and descriptive subject up to the decade of the 1960s. Witness two of the most influential texts of that time: Andrewartha and Birch (1954), an excellent book but explicitly antithetic to theory in the form of anything resembling a mathematical model; Odum (1953), arguably foreshadowing aspects of 'systems ecology' with its insightful focus on patterns of energy flow in ecosystems, but with the emphasis descriptive rather than conceptual.

For evolutionary studies as well as for ecological ones, we think the 1960s saw a change in the zeitgeist. For evolution, much of the stimulus derived from Bill Hamilton's conceptual advances. For ecology, it was the reframing by Evelyn Hutchinson (1965) and his student Robert McArthur (1972; see also MacArthur and Wilson, 1967) of old questions in more explicitly analytic ways; one could perhaps say, rephrasing them in the idiom of theoretical physics. How similar can species be, yet persist together? What tends to govern the number of species we see on an island, and how does this number depend on the size and isolation of the island? Gilbert White's question of population abundance was revisited—and expanded beyond the sterile controversies of the 1950s about whether populations typically are governed by tight density dependence or fluctuate greatly under the influence of environmental factors—to ask the more precise dynamical question of why do some populations remain relatively steady, others show regular cycles, and yet others fluctuate wildly? Given the observed patterns of relative abundance of the different species in particular communities, what are the underlying causes? What is the relation between the complexity of a food web (variously defined) and its ability to withstand disturbance, natural or human created?

These more deliberately conceptual or theoretical approaches differed from early work, in our view, in that they went beyond the codification of descriptive material, and the search for patterns within such codification, to ask questions about underlying mechanisms. To ask questions about why, rather than what. Mathematics enters into such studies, essentially as a tool for thinking clearly. In pursuing a 'why' or 'what if' question about a complicated situation, it can be helpful to ask whether particular factors may be more important than others, and to see if such insight or guesswork does indeed provide testable explanations. Mathematical models can be precise tools for doing this, helping us to make our assumptions explicit and unambiguous, and to explore 'imaginary worlds' as metaphors for such hypothetical simplicity underlying apparent complexity. The 1970s saw much activity of this kind in ecological research, helped in part by basic advances in our understanding of nonlinear dynamical systems and by the advent of increasingly powerful and user-friendly computers.

In particular, the phenomenon of deterministic chaos received wide recognition in the 1970s. The finding that very simple and purely deterministic laws or equations can give rise to dynamical behaviour that not merely looks like random noise, but is so sensitive to initial conditions that long-term prediction is effectively impossible, has huge implications. It ends the Newtonian dream that if the system is simple (very few variables) and orderly (the rules and parameters exactly known), then the future is predictable. The 'law' can be as trivial as $x(t+1) = \lambda x(t) \exp[-x(t)]$, with λ a known and unvarying constant, but if λ is big enough then an error of one part in one million in the initial estimate of $x(0)$ will end up producing a completely wrong prediction within a dozen or so time steps. Interestingly, it is often thought that chaotic phenomena found applications in ecology after others had developed the subject. In fact, one of the two streams which brought chaos centre stage in the 1970s derived directly from ecological research on models for a single population with discrete, non-overlapping generations. These models were first-order difference equations; the other strand was Lorenz's metaphor for convective phenomena in meteorology, involving more complex—although still relatively simple—three-dimensional differential equations.

Advances in computing have also been of great help in all areas of ecology: statistical design of experiments; collecting and processing data; and, coming to the present book, developing and exploring mathematical models for both simple and complicated ecological systems. There are, however, some associated dangers, which deserve passing mention. The understanding derived from computer studies of complicated models can sometimes be substantially less complete than that gained from the analytic methods of classical applied mathematics and theoretical physics. The early days of computers—mechanical calculators—saw them used by theoretical physicists in conjunction with analytic approximations, to explore previously intractable problems. The result, however, was that at every step there was preserved an intuitive understanding of the relation between the underlying assumptions and the results. In contrast, many scientists who today use computers to explore increasingly complex mathematical models have little formal background in mathematics, or have forgotten what they were once taught. Most of this work is interesting and excellent. But, absent any degree of intuitive understanding of how the input assumptions about the system's biology relate to the consequent output, we need to be wary (May, 2004). Too often, an 'emergent phenomenon' means little more than 'I've no clue what is going on, but it looks kinda interesting'. Happily, there are very few examples of this in ecology. More particularly, throughout the present book we aim, wherever possible, to provide intuitive understanding of the lessons learned from mathematical models.

Be all this as it may, there has been a marked rise in theoretical ecology as a distinct sub-discipline over the past three decades or so. Many of the practitioners are not to be found in the field or laboratory; a greater number, however, find their experimental contributions in field and/or laboratory to be inextricably interwoven with their theoretical and mathematical contributions. Ecology has come a long way from the 1970s, when a few empirical ecologists resented outsiders, who had not paid their dues of years of toil in the field, presuming to mathematize their problems (often sweeping aside arguably irrelevant, but certainly beloved, details in the process). Others perhaps welcomed the intrusion too uncritically.

The end result, however, is seen clearly by comparing today's leading ecology texts with those of the 1950s and 1960s. In the latter, you will find very few equations. Today, in contrast, you will find a balanced blend of observation, field and laboratory experiments, and theory expressed in mathematical terms. The comparison, for example, between the first edition of Begon, Townsend and Harper (1986) and the earlier Andrewartha and Birch (1954) or Odum (1953) is pronounced. We think this marks a maturation of the subject, although there undeniably remain large and important areas where there are still more questions than answers.

1.1 This book and its predecessors

This book (TEIII) is essentially a greatly transmogrified version of one first published in 1976 (TEI), and followed with substantial changes in 1981 (TEII; this was not a perfunctory update, but had three chapters completely re-written by different authors, two new chapters added, and all others revised; TEI's 14 chapters involved 11 authors, TEII's 16 chapters had 13 authors, of whom nine were from TEI). This new version, 25 years on, has 15 chapters by 23 authors, only three of whom are veterans of TEII.

Like the previous two, this book is not a basic undergraduate ecology text, but equally it is not a technical tome for the front-line specialist in one or other aspect of theoretical ecology. Rather, the book is aimed at upper-level undergraduate, postgraduate, and postdoctoral students, and ecological researchers interested in broadening aspects of the courses they teach, or indeed of their own work. As such, we think it fair to claim that TEI and TEII in their own time played a part in the above-mentioned transition in the general subject of ecology, where earlier texts, in which mathematical content was essentially absent, contrast markedly with today's, where theoretical approaches—sometimes explicitly mathematical and sometimes not—play an important part, although no more than a part, of the presentation of the subject. Some of our acquaintances, indeed, still use the earlier volumes as supplements to their undergraduate courses. TEII, although out of print, still trades actively on the online bookseller Amazon.

This book, on the other hand, differs from the previous two by virtue of these changes in how the subject of ecology is defined and taught. Much of the material in TEI and TEII would now, 25 years and more on, be seen as a routine part of any basic