

Preface

This is an introductory textbook on mathematical ecology bridging the subdisciplines of population ecology and ecosystem ecology. The expected reader is you: a beginning graduate student, advanced undergraduate student, or someone who thinks of themselves as a student all their lives, with a working knowledge of basic calculus and basic ecology. While this is intended as a stand-alone text, the level is such that once you have read through it, you will be able to read more advanced texts and monographs such as Ågren and Bosatta (1998) and Kot (2001) with greater depth. While there are other very good introductory texts in mathematical ecology (e.g., Edelstein-Keshet 1988 [reissued but not revised 2005], Yodzis 1989 [now out of print], Gotelli 1995, Roughgarden 1997, Case 2000, and Kot 2001 are among the most widely used), none bridge the gap between population ecology and ecosystem ecology.

Ecological problems are complicated in ways that our language has not evolved to handle. Mathematics provides a more precise way than the spoken word of thinking and talking about the rates of change, nonlinearities, and feedbacks characteristic of populations and ecosystems. Even Edward Abbey, one of the sharpest thinkers who never solved an equation, once said: "Language makes a mighty loose net with which to go fishing for simple facts, when facts are infinite."^{*} It is my hope that mathematics can help us tighten that net a bit, allowing us to catch a few facts that may have otherwise slipped through. At the very least, mathematics has precise tools for handling the infinite.

For the past 12 years, I have given courses in mathematical ecology and ecosystems ecology during alternate fall semesters. Often, the major topics of our discussions in each of these courses concern the relationships between population dynamics, species, and ecosystem processes such as productivity, nutrient cycling rates, and input-output budgets. These are leading research questions in ecology and have been major interests of mine for the past 25 years.

These are intellectually challenging questions. It is often easy to make a "plausible" argument that some hypothesized relationship between populations, species, and ecosystems must be true, only to find on more rigorous examination that it is not necessarily true, true only under certain restrictions, or simply not true at all. Framing the plausibility argument in mathematical terms and using the rules of mathematics to examine its logical structure is often the best way to uncover the sense in which it might be true. In fact, the mathematical examination of these arguments often uncovers hidden assumptions; these in turn suggests new experiments to determine

^{*}*Desert Solitaire*, Author's Introduction.

whether they hold in the "real" world or new theoretical investigations to determine what happens when such hidden assumptions are relaxed in different ways.

Questions about the relations between populations and ecosystems are also challenging because the cultures of population ecologists and ecosystem ecologists differ so much. In part, these differences between population and ecosystem ecologists arise in their graduate training. Population ecologists are often trained to analyze the dynamics of populations' and species' interactions using analytical mathematical methods which allow them to calculate algebraic expressions for equilibria and their stability.

Because population models focus on the dynamics of collections of live individuals, death is often treated as an export from the system. By contrast, the ecosystem ecologist considers dead material to still be in the system, simply be detached from the live populations and subject to different rules. Eventually, through microbial decay, the dead material is transferred to the resource pool which is then taken up by plants.

Because of the large number of compartments they generally consider and measure, ecosystem ecologists have not usually used analytical mathematical methods. Instead, large and complicated computer simulation models have traditionally been their method of choice in analyzing and synthesizing ecosystem data. Although these simulation models may make quite accurate predictions for specific situations, they are often almost as complex as the system being studied. Therefore, it is sometimes difficult to understand why their predictions are as they are, leading to an interesting paradox in which accurate prediction may not be the same as general understanding. Furthermore, through their investigations into the origin of chaos in single-species models, population ecologists have taught us that we can have understanding without predictability, a conclusion accepted with reluctance by some (but not all) ecosystem ecologists.

Therefore, ecosystem ecologists and population ecologists have been trained to speak different languages. Population ecologists have traditionally ignored nutrient feedbacks to populations through litter and its decay, whereas ecosystem ecologists traditionally dismiss analytical approaches in favor of simulation models. This lack of a common language or approach amongst population and ecosystem ecologists may impede our ability to address important practical problems. It is no wonder that many ecologists find the relationship between populations, species, and ecosystem properties extremely difficult to understand: each group has part of the answer but they find it difficult to speak to each other and frame questions in a common language.

In spite of the traditional dichotomy of using either simple analytical models of a few species or complicated simulation models of whole ecosystems, it is possible to couple interactions between species and the flux of an inorganic resource by simplifying the ecosystem to only a few compartments so that we can use analytical mathematical techniques to gain understanding about system behavior, especially how ecosystem properties emerge from an interaction between populations and the flux of inorganic resources. In this book, the same mathematical techniques will be used as a common thread to help unify population and ecosystem ecology.

These mathematical techniques are also essential for exploring how changes in controlling factors across thresholds often cause rapid changes between different states of an ecological system, which are sometimes called "regime shifts" (Scheffer et al. 2001). These rapid changes between different states are often accompanied by the

appearance of new behaviors, such as limit cycles, extinction of species, or changes in top-down and bottom-up controls. Some examples of current interest are the possibility of rapid change in communities and ecosystems with slowly rising temperatures once some critical value of temperature is exceeded, the rapid changes in communities once critical thresholds of nutrient inputs are exceeded, and the rapid changes and extinctions in populations once critical values of harvesting rates are exceeded.

Different states of populations, communities, or ecosystems often correspond to different equilibrium solutions of a model. In turn, these solutions are often separated by a critical value of a parameter or a function of several parameters. Rapid changes in the nature and stability of solutions of equations as critical parameter values are crossed are known mathematically as bifurcations. Bifurcations between different equilibrium solutions appear suspiciously like the rapid changes in nature as controlling factors cross critical thresholds. Examples of bifurcations which we will meet in this book include: (i) saddle-node bifurcations, separating persistence from extinction of a species once a critical harvesting rate is exceeded; (ii) transcritical bifurcations, leading to shifts between two different communities once critical inputs of a limiting nutrient are exceeded; (iii) Hopf bifurcations, leading to stable limit cycles once critical values of carrying capacity are exceeded, otherwise known as the "paradox of enrichment" (Rosenzweig 1971); and (iv) Turing bifurcations, leading to the appearance of spatial patterns once critical values of diffusion rates of populations are exceeded. We shall explore examples of these and other bifurcations and their ecological implications throughout this book.

Bifurcation theory is therefore a powerful mathematical technique to help us understand sudden and interesting changes in the behaviors of ecological systems as some parameter or combination of parameters pass some critical value. Bifurcation theory draws heavily on the theory of eigenvalues and Jacobians and, insofar as bifurcation theory seems a promising mathematical approach to understand rapid changes in nature, one must have some grounding in eigenvalue analyses – indeed one must be able to frame questions and construct systems of equations with the use of these techniques in mind.

The purpose of this textbook is therefore to help you develop your thinking to bridge population and ecosystem problems using the mathematical tools of eigenvalue analysis and bifurcation theory as common threads. To successfully do this, you need a working understanding of calculus, especially the concept of limits; linear algebra, especially matrix operations required to analyze populations with age or stage structure or multiple species models; and differential and difference equations, especially the analysis of model stability by means of eigenvalues and eigenvectors. While all ecology graduate students have had training in calculus, it may have been a while since they used it; a few have had experience of linear and matrix algebra; very few have been exposed to eigenvalues and eigenvectors. Accordingly, Chapter 2 is a "mathematical toolbox" laying out the tools to be used in this book and providing some exercises for you to practice using these tools without much reference to any biology at first. This lays the foundations for a mathematical vocabulary for the book. Many of these exercises will appear later in more ecological form.

I try whenever possible to derive the standard equations of mathematical ecology from some more fundamental "first principles" of birth and death, probability of two individuals meeting, and conservation of matter. Typically, these derivations are

motivated by uncovering or relaxing some "hidden assumption" to address an unrealistic behavior in some prior, simpler model. In addition, intermediate steps in these derivations often shed some light on what the final equation means: a lack of understanding of where the final equation came from can lead to misleading analogies and conclusions. In addition, many derivations and proofs often depend on some trick or turn of an argument in an intermediate step, and learning these tricks or turns of an argument both enriches the ecological and mathematical underpinnings of a model and often proves useful in derivations of other models.

Every chapter begins with an introduction to a new problem, usually motivated by some problems unearthed in the previous chapter or chapters. These problems are usually an unrealistic biological behavior of the previous, simpler models. We then try to uncover the assumptions that may be responsible for the problem behaviors. The chapters usually proceed by mathematically relaxing these assumptions in different ways and analyzing how this improves the model's behavior (or not).

Every chapter ends with two sections, the first entitled: "Summary: what have we learned?" which, besides the obvious summarizing of the main points, also brings the discussion back to a wider plane. The final concluding section of each chapter (except the Introduction and Mathematical Toolbox) is a section called "Open questions and loose ends." Here, I point you in some directions and towards some papers or texts about problems that lack of space does not allow me to go into. I also suggest some open questions for you to consider. Some of these are small questions for you to explore, perhaps as additional homework problems, but they may lead to larger questions. Some of these are large open questions (such as control of chaos in population models) which are at the current edge of research. I hope that these may help you choose a thesis problem (if you are a graduate student) or research problem (if you are already establishing your own program). I would welcome learning from you any findings along these lines or about any papers that have addressed them that I may not know about (and for which I apologize to the authors).

By introducing you to the mathematical tools required to analyze models of populations, communities, and ecosystems, I hope to help you develop more rigorous ways of thinking about the interaction of population and ecosystem dynamics. It is my further hope that these ways of thinking will spawn more creative approaches to these problems.

I have learned much by writing this book: oftentimes, connections have emerged that neither I nor (I believe) anyone else has seen before. If you are already a professional mathematical ecologist or mathematician, I hope that these connections will surprise you as much as they did me. If you are a student, I hope you will learn as much or more than I did and, in turn, teach me through the papers you will write.