PREFACE

When ecology emerged from the general subject of biology, it did so in the tradition of the world's great naturalists—Maria Sibylla Merian, Thomas H. Huxley, Alfred Russel Wallace, Charles Darwin, and others. When Ernst Haeckel finally coined the term "ecology," the field was little more than what natural history had always been, the detailed study of the way organisms interact with one another and their environment, a series of fascinating stories about nature. Use of quantitative techniques was minimal. Larry Slobodkin, one of the pioneers in the development of theory, once quipped to a class that an ecologist is "someone who wears khaki pants, doesn't know much about mathematics, and misidentifies local beetles."

Indeed, maturation of the field emerged from a more serious mathematical approach. The foundational equations of Lotka and Volterra were invented in 1926, and their application to a laboratory system by Gause was complete by 1935. Yet what turned out to be foundational was largely ignored until the late 1960s, when Robert MacArthur, Richard Levins, and Robert May began their illustrious careers, with many others to follow. Mathematically based theory became an acceptable, even essential ingredient, with increasingly sophisticated theoretical approaches.

As a consequence, the average ecology student today faces some daunting literature. The legacy of the late 1960s and early 1970s has been a fascinating, yet sometimes perplexing, collection of theoretical approaches that have transformed the field dramatically. A course in ecology today is as likely to contain complicated differential equations as descriptions of life histories, a dramatic change from the situation 40 years ago, when mathematics was little mentioned. And observational studies as much as experiments now rely on predictions from abstract theory. Ecology has become a remarkably exciting discipline principally because of this burgeoning theoretical superstructure.

Along with the momentum derived from this paradigm shift, we also see some lingering frustration as students confront this literature. In our experience, this frustration is frequently derived from a less than adequate appreciation of what have become the fundamental quantitative principles of ecology. In this book we have attempted to present these fundamentals in as heuristic a way as possible.

But precisely what are those fundamentals? Attempting to summarize the underlying quantitative framework for the entire field of ecology can be frustrating. Indeed, the content of a course in "general ecology" at a U.S. university may vary considerably. We found the choice and arrangement of subject matter only loosely correlated when comparing recent texts. This variability is, we believe, the consequence of the youthfulness of our science. Although this may seem frustrating to some, it is a source of excitement for most in the field.

Nevertheless, there is one subdiscipline of ecology that seems to have developed a canon. Virtually all courses that contain *population ecology* in their titles cover essentially the same material. In this one corner of the field, ecologists seem to agree on what constitutes the basic subject matter. And any survey of contemporary literature in ecology will uncover one or more of the basic ideas of population ecology underlying almost every published study.

In this text we attempt to present these first principles of population ecology. The book is intended as a text for advanced undergraduate and beginning graduate students, and it focuses on the analytical details of the basic subject matter. It is not at all intended to be an introduction to the literature. Individual applications are chosen as examples of the models and techniques presented and are not intended to be the best or the best-known studies in the literature—they are simply examples. Indeed, a review of the literature of "population ecology" would fill several volumes and would likely not serve much purpose anyway. In this book we have not made such an effort.

Although the subject matter of population ecology and thus this book is highly mathematical, the material is presented in such a way that only introductory calculus and a basic understanding of linear algebra are necessary prerequisites. For those students far removed from their calculus class, a basic understanding of the nature of a derivative and an integral plus the ability to differentiate simple functions (polynomials and exponentials) is really all that is required to fully appreciate this basic material. On the other hand, many students of ecology do not come to the field with a proper background in the basic operations of linear algebra. For these students we include an appendix at the end of Chapter 2.

This edition of the book includes an extensive set of exercises peppered throughout the text. These exercises are intended to encourage the student to think about the development of the text *before* that development happens. The exercises range from trivially simple to frustratingly complex. Our experience is that the attempt to solve a problem is the pedagogically important part of an exercise. We encourage students to develop their own style of dealing with the exercises, ranging along a continuum. At one end, simply ignore the exercises. The text is, like the previous edition, intended as a complete document without the exercises anyway, so students who wish to receive only a superficial introduction or students who feel especially confident with the material and wish only to have their understanding of the subject refreshed can easily skip all of the exercises. At the other extreme of the continuum, it is, we feel, worthwhile to attempt to do each of the exercises before reading on. As in the case of any quantitative approach, the exercises may sometimes be frustrating, especially if one begins thinking about them in the wrong direction. We thus recommend that when an exercise begins to seem intractable or when frustration begins, even at the initial formation of the answer, the student move to the answer sheet (which is supplied at http://www.sitemaker.umich.edu/jvander/home in the form of an editable spreadsheet). Most of the answers are evident just from examining the worksheet. But it may be more useful for some students that the formulas in the cells of the spreadsheet can be easily manipulated by anyone with a knowledge of basic spreadsheet operation. The ability for such manipulation provides the student with the option of experimenting with various parameter values and starting conditions from which to empirically explore the subject matter of the exercise.

The organization of the book is based on chapter 1 as a foundation. With the exception of chapters 8 and 9, which depend to some extent on material from chapter 6, the rest of the chapters could stand alone after chapter 1 has been read. Chapter 2 enlivens the subject matter of chapter 1 with the reality that most populations in nature have some sort of structure. Further elaborations of this introductory material can be found in Caswell's excellent text (Caswell 2001). Chapter 3 follows with some simple applications of chapters 1 and 2 to some theoretical and practical issues. Chapter 4 introduces to the basic models nonlinearities—a subject that has witnessed an explosion in the literature—although most of the treatments are rough going mathematically. References that should be accessible to most ecology students are the two-volume set by Jackson (1991), the less inclusive but perhaps simpler text by Alligood et al. (1996), and, perhaps the most enlightening, the general text by Strogatz (2001). Chapter 5 deals both with statistical descriptions of spatial aggregation of individuals and populations and with population-dynamic models that incorporate spatial information either as foundations for the dynamics (e.g., metapopulations) or as consequences of the dynamics (reaction/diffusion equations). Spatial statistics is a burgeoning field, especially with the explosive growth in the use of geographic information systems. Our treatment is elementary, and students interested in this subject need to consult more sophisticated treatments (e.g., Diggle 1983; Fortin and Dale 2005). Metapopulation theory is introduced in its traditional form strictly as a mean field theory, and spatial pattern formation uses a simple qualitative presentation of reaction/diffusion equations. More detailed elaborations of the metapopulation concept can be found in the monograph by Hanski (1999), and the formation of spatial pattern is explored in several chapters of the volume edited by Dieckmann et al. (2000).

Finally, chapters 6–9 are introductions to two-species interactions. Chapter 6 deals with positive–negative interactions generally, specifically formulated as predator–prey interactions. More sophisticated treatments of this material can be found in the many applications of predator–prey theory in the literature, but we know of no particular text that treats advanced predator–prey theory as such. Useful applications can be found in Hawkins and Cornell (1999). Epidemiology is really the conceptual application of predator–prey theory to microparasites, but the framework that is used is basically that of metapopulations, as discussed in chapter 7. The standard reference on this material has become Anderson and May (1991), and a more recent and more compact summary can be found in Keeling and Rohani (2008). Chapter 8 deals with interspecific competition. More complex elaborations of the material presented in this chapter can be found elsewhere (e.g., MacArthur 1972; Tilman 1982; Chesson 2000). Finally, chapter 9 briefly outlines the fundamental theoretical ideas of facilitation and mutualism.

All of the material in this book has been presented to several groups of graduate and advanced undergraduate students at the University of Michigan. We owe a debt of gratitude to those students for their contributions to improvements that led to the present text. We also wish to thank our colleagues Mark Wilson, who contributed substantially to initial drafts, as well as Mercedes Pascual, Annette Ostling, and Aaron King, who were kind enough to use it in their classes. Special thanks to Dave Allen, Doug Jackson, Ed Baskerville, and Gyorgy Barabas for pointing out errors and better ways of presenting things over the years.