

PETER HAZIS

Introduction to

Theoretical Ecology

INTRODUCTION TO THEORETICAL ECOLOGY

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*This book is dedicated,
With thanks,
To my parents.*

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INTRODUCTION TO THEORETICAL ECOLOGY

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Preface

I have been lecturing on theoretical ecology regularly for the past ten years, first at the University of Zürich, Switzerland, then at the University of Guelph. When I began lecturing in Zürich, it was suggested that I provide a "*Scriptum*" to go with the lectures, in keeping with European academic custom. When I moved to Canada I continued updating and refining these "prepared lecture notes," as there was no book I could use as a "textbook" in the North American sense.

Over the years many people suggested that it would be useful to publish the notes for a wider public, but I resisted this notion, mindful that it would entail an order of magnitude more work on my part. But as the lecture notes evolved, on the one hand, and I became increasingly aware, on the other hand, of widespread misunderstanding among ecologists as to the nature and functioning of theory, my resistance weakened. The result is the present volume.

The writing retains something of the informal, "conversational" character of its lecture note forebears. The audience I have in mind is mainly students of ecology with empirical interests, though I would hope that a budding theorist could find inspiration here as well. A very strong attempt is made to communicate mathematical thinking to people who may not by nature find this way of thinking very natural—the reader is "taken by the hand" far more than is customary in mathematical writing.

The book contains the basics (and somewhat more) of population, community, and life-history theory. It does not attempt a comprehensive survey of theoretical ecology. Relatively few topics are covered, but those that are covered are treated in considerable depth. A text with comprehensive coverage would have to be either impracticably immense or impenetrably condensed. My aim, instead, is to give students a deep enough understanding of the topics that are

discussed to enable them to pick up other areas of interest (including new developments) from the primary literature.

I have not discussed data analytic techniques such as mark-recapture and so on, but the book of Krebs (1989) is dedicated to this topic. I have also not treated the ecology of infectious diseases, except for one example, as this topic has been cogently reviewed by Anderson (1981) and Anderson and May (1985). Similarly, Clark (1976) is a superb introduction to management problems. The volume edited by May (1981c) covers a number of other topics that I have not touched upon, and May's volume will be accessible to the student of this book.

I have written for advanced undergraduates or graduate students. In particular, I presuppose one or two years of ecology and a year of calculus. Thus, for example, I start out by simply writing down the logistic equation, assuming it is familiar to the student. There is an appendix that discusses certain mathematical topics beyond first-year calculus, which are used in isolated places in the main text. These places are all flagged, and the book is written so that the reader who does not wish to go quite so deeply into mathematics can skip over them (and the appendix) and still follow the gist of the argument.

As well, quite a lot of mathematical material—indispensable, to my mind—is developed within the main text. While this does to some extent interrupt the flow of biological ideas, I did not want to segregate the mathematics so much that the student would fall prey to the temptation to just “take my word for it.” I believe students will find they can view ecology from a theoretical perspective much more tellingly if they really understand the theory for themselves and don't have to view theoretical results as Pronouncements. The basic spirit of the book is that advocated by Albert Einstein: “Everything should be made as simple as possible—but not simpler.”

I think it is vital that we develop a common understanding in ecology as to what constitutes a scientific explanation (within the particular science of ecology), and what are valid protocols for research that aims at such explanation. To get the student thinking along these lines, I have explicated some methodological basics, especially pertaining to pluralistic (introductory paragraphs to Chapter 6, and Section 6.4) and probabilistic (Section 8.1.2) explanations.

Because the variability from one institution to another in the students' preparation for this kind of course is greater than in the more standard biological fare, it is impossible to estimate how much of the book can be covered in a given time. The book probably contains enough material for a one-year course at most universities. Parts One and Two form an integrated unit that must be taken in the order given. Part Three is essentially independent. Thus a one-semester (or, with supplementation, possibly a year) course in theoretical population and community ecology could be based on Parts One and Two, or a one-semester course in life-history theory could use Part Three. The minimum that should be covered in Parts One and Two is Chapters 1 through 6. Chapters 7 and 8 could be included if time permits, or left for students to read on their own. (Or, one might want to cover Chapter 9 instead.) The minimum that would constitute a reasonable treatment of life-history theory is Chapters 9, 10, and 13.

To mention one further element of flexibility: some instructors might find that their students are happier to start with Part Three (which is mathematically simpler), then go on to Parts One and Two. I have put Part Three at the end because I feel that this topic is less well founded than the others, because of the pervasive use in it of problematical optimization arguments. The difficulties in the optimization program are discussed at the very beginning of Part Three.

Pictorial material is dealt with here in a somewhat unusual way, which I should perhaps explain. The book contains figures that are placed on the page and labeled in the usual way, and “sketches” that are integrated directly into the text. The hope is that treating the sketches in this way will aid in the flow of the argument. Basically, the sketches are things that would be drawn on the blackboard in a lecture; they are virtually an integral part of the text, and are so presented here.

The book includes exercises. These are almost entirely mathematical calculations. Most of them fill in gaps in the text and are included in the text at the appropriate places. Additional exercises, which extend the text, are given at the ends of chapters.

Some students complain that a lot of the exercises, especially among those that fill in gaps, are boring and routine. In some cases this is because the exercises in question really are too easy for the student. Sometimes, though, the student just does not want to plod through the preliminaries. The painful truth is that you must learn to walk before you can dance; you have to master scales and arpeggios before you are ready to attempt sonatas.

The student who wants real mastery of this material should do all the exercises; the instructor has, of course, the option of setting a mandatory standard short of this, or indeed of adding more exercises. I have even taught the course with *no* assigned exercises. These students wrote nonmathematical term papers that applied the ideas developed in the course to systems that they were familiar with or particularly interested in.

Some of the exercises are computer projects, and here, again, there will be a lot of variability from one institution to another in the appropriateness of such exercises.

I should make one more point about the exercises that fill in gaps in the text. In mathematical writing, it is quite common to sketch how a calculation or proof is done, without giving all the details. Serious readers will often fill in these details as they go along (at least, on second or third reading), and this is certainly to be recommended to students. By calling attention to these gaps in the form of exercises at the places where gaps occur, I hope to train the student to spot places where an argument needs to be rounded out.

Ultimately, the idea of writing this book originated with Hans Burla, who invited me to lecture on theoretical ecology in Zürich and suggested writing a *Scriptum* for the course of lectures. As well, I have spent many happy hours discussing biology with Hans. Several generations of students, both in Zürich and in Guelph, forced me to think clearly with their questions, kept me honest with their skepticism, and encouraged me with their interest. I wish I could name

them all, but I do need to mention two excellent students, Dominique Anfossi and Susan Glenn, who provided detailed criticisms of late versions of the lecture notes.

I am very grateful to Ted Case, Joel Cohen, Jim Drake, Mike Gilpin, Robert Holt, Dave Lavigne, Sandy Middleton, Bob May, Craig Pease, Georg Ribi, John Roff, and David Tilman for their comments on the manuscript or parts thereof. Special thanks to Don DeAngelis for his very thorough criticisms. And my very special thanks to family, friends, and colleagues for their patience and encouragement.

Peter Yodzis

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Introduction

Science is an attempt to understand the world around us. In part, it proceeds by very carefully, very precisely, very thoroughly describing what we observe. But, while description is the ultimate foundation of science, it is not enough. For our world—indeed, almost any given small part of it—is very, very (some would say boundlessly) complex and diverse. Eventually description, in itself, overwhelms.

So scientists seek patterns in the data. One way of doing this is to scrutinize the data themselves, sometimes utilizing sophisticated statistical methods. This kind of analysis, too, is an important part of science, but it is still not enough. How do we know what kind of pattern to look for? Could it be that some patterns in the data are too subtle for ad hoc scrutiny to detect?

Moreover, even when we do see pattern, we may wonder what *causes* it, whether we can explain it in terms of some underlying principles or processes. The contemplation of underlying causes, by accounting for discerned patterns in the data, may please our desire to understand. Furthermore, it may suggest to us new kinds of pattern to look for in the data (and new kinds of data to gather in the first place). This is the scientific activity that we call *theory*.

Theory proceeds by making assumptions about how things work, assumptions that simplify the vast complexity of nature by abstracting out certain features that the theorist regards as essential. It then deduces the consequences of these assumptions—and comparing these consequences with observed data is a way of looking for pattern in the data.

Ecological theory has over the past few decades made very extensive use of mathematical models, and since this sort of approach is perhaps a bit unfamiliar to many biologists, I am going to start out with a few general remarks about mathematical models.

1.1 MODELS

First, what is a model? *Webster's* defines it as "a hypothetical or stylized representation," and I think this is an excellent characterization of the sense in which the word is used in science. The purpose of a model is not to provide a literal *description* of some system, but to provide a *conceptualization* (representation) of the system and its workings, in terms of which one can think about the system and understand something of its behavior. Any model will inevitably be incomplete and even false in some respects, but in discovering these defects we often learn new things about the system—and come up with new and better models.

A common misconception about mathematical models is that it is characteristic of them to very much simplify the actuality being investigated. It is true that mathematical models simplify very much. But this is not characteristic of mathematical models—it is characteristic of *any* attempt to comprehend the world. For instance, even decades of intensive empirical study of an ecosystem leave us with a simplified view of the system. The real issue is: How much simplification, and what kind of simplification, is it sensible for us to make? Right now, we in ecology are still very far from being able to address this issue conclusively.

Models can be expressed in several different ways: verbally, in graphs or diagrams, or mathematically. In current theoretical ecology, while verbal, graphical, and diagrammatic models are often used in preliminary formulations of ideas, it is seldom long before the train of thought finds expression as a mathematical model.

There are two reasons for this prevalence of mathematical models in ecology. First, the systems being studied in ecology tend to be very complex, and mathematics is ideally suited to the expression of complex relationships in a form that makes it relatively easy to work out the consequences of these relationships. In principle, one could attempt to do all the same reasonings verbally, or in some extraordinarily complicated diagram, but in practice this would be far too mind-bogglingly confusing.

Second, mathematics is very exact. It forces one to (try to) say *exactly* what one's ideas are, and it enables one to find out *exactly* what their consequences are. Mathematics is not the only form of clear thinking, but it is the most powerful, and it imposes a certain discipline which helps to keep one from sliding into fuzzy thinking.

It is not inconceivable that the phenomena of ecology are just not amenable to such a rigorous approach. Theoretical ecology, while enjoying a measure of success, has yet fully to prove itself. But the promise is too great to be ignored. The scientific spirit—to say nothing of the urgency of the environmental crisis—demands that we explore this promise to the fullest.

One should be aware that two quite different kinds of models are commonly used in ecology (and elsewhere). C. S. Holling (1966) uses the terminology "tactical" and "strategic" to distinguish the two kinds of models.

A tactical model in Holling's sense is a very detailed model of a very

specific system. Such a model is often referred to as a “simulation” because its aim is to mimic as closely as possible the detailed actual behavior of some particular system. Because it attempts a highly detailed and realistic representation, such a model is immensely complicated and can be handled only on a substantial computer.

The tactical approach probably seems the more natural to many biologists, and yet it is, I think, fair to say that this approach has contributed little to ecological theory, in comparison with the strategic approach. This is because tactical models are so terribly specific that it is difficult to extract general insights from them; and they are so complicated that calculations with them are cumbersome and not at all transparent. Nevertheless, these models can be vital tools when one’s goals are sufficiently concrete and specific, and one has at one’s disposal the extensive resources that are required to build a reliable tactical model. A number of excellent books with a tactical orientation are available (for instance, Watt 1968, Patten 1971, Hall and Day 1977).

The strategic approach is a little harder to describe. It will be my approach throughout this book, so you will become familiar with it anyhow if you just read on. The basic idea of this viewpoint is to sacrifice detail for generality. One tries to build relatively simple models that, while not taking into account every detail of any one system, do capture the *essence* of *many* systems. Such an approach lends itself very well to the perception and formulation of general insights, largely because it is predicated on the assumption that such insights can be had!

It is, however (as Holling himself is at pains to emphasize), far too crude to draw an absolute binary distinction: tactical or strategic. It makes more sense to think of each model as lying somewhere in a continuum of approaches, with “tactical” and “strategic” as the two extremes (or, more precisely, as the two “directions” in this one-dimensional continuum). One can, as we shall see, add or subtract bits of detail to or from a model in order to strike the right balance between detail and generality, between thoroughness and workability.

1.2 ON THE RELATION BETWEEN THEORY AND OBSERVATION

I am not going to discuss much data in this book. I am just going to discuss theory for the most part, and will leave it to each reader to fill in examples from his or her other studies in biology and ecology, and experience of particular organisms.

When I do discuss data, it will be to illustrate the relation between theory and observation. This is a very important relationship; indeed it is crucial to the scientific enterprise. I would like to suggest to you at this point a couple of vague generalities to keep in mind as we go along.

Most observers develop hypotheses about their systems and try to test these hypotheses. Often they start work on a system with some hypothesis already in

mind. Now, one function of theory is to *sharpen hypotheses*. This process of sharpening hypotheses can take two forms: it can involve making the hypotheses themselves more precise, or it can involve pinpointing just exactly which measurements need to be made in order to test the hypotheses (perhaps most efficiently in some sense). Or it can involve both these aspects.

But there is another, more subtle and marvelous, function of theory. As I hope you will see in the rest of this book, a theory has a sort of life of its own, a course of development that flows from its inner logic. And in the course of this process the theory will often *generate new hypotheses*, which, often enough, can be tested in the field or lab.

PART ONE

THE GROWTH OF SINGLE POPULATIONS

The growth of a population depends upon many factors. Some of these are abiotic characteristics of the environment, some are characteristics of the population itself, and some arise from interactions with other populations. We begin our study of ecological theory by considering the growth of a population for which interactions with other populations are negligible.

There are, to be sure, precious few, if any, populations in nature for which interactions with other populations are *completely* and *utterly* absent. But it is often enough a reasonable first approximation to neglect interspecific interactions. Moreover, we shall make the acquaintance in this relatively simple setting of a host of important concepts whose usefulness extends far beyond the single-species situation.

I will make some additional simplifying assumptions in this part. I will assume unless otherwise stated that all abiotic factors remain constant (no seasonal or random environmental fluctuations). Environmental fluctuations are discussed in Sections 2.4 and 3.6. I will also neglect age structure within our populations (until Part Three, where I discuss age structure), as well as all phenotypic variation. I will assume further that we are dealing with populations that lack any spatial structure (until Section 5.4). In short, at first we consider populations that are homogeneous in every respect: the state of such a population will be specified by a single function of time: the density (number or biomass per unit area or volume) N .

These are a lot of simplifying assumptions, but they will enable us to get started. As indicated in the preceding paragraph, we later drop some of these simplifications. But even at our present level of simplicity, we will gain some fascinating insights from these models.

Under certain circumstances (explicated in Section 2.5) it is appropriate to view population growth as a continuous process in continuous time (Chapter