ECOLOGY

THEORIES AND APPLICATIONS

SECOND EDITION

PETER D. STILING

Ecology: Theories and Applications

Second Edition

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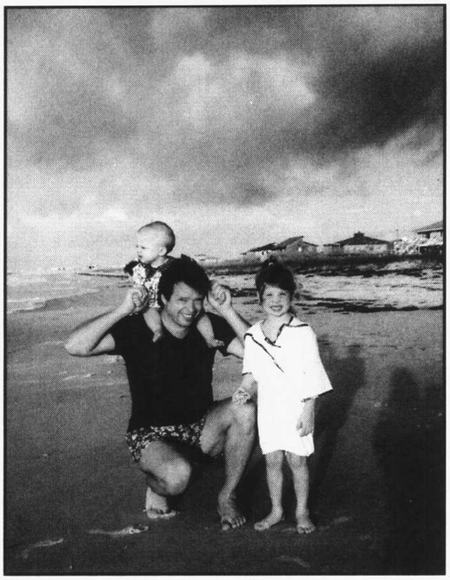

The photograph shows the author with daughters Zoe and Leah at the coast, near his field sites.

About the Author

Peter Stiling is an associate professor of biology at the University of South Florida, Tampa. He has taught classes in Ecology, Environmental Science, and Community Ecology, and in 1995 received a teaching award in recognition of classroom excellence in these areas. Dr. Stiling obtained his Ph.D. from University College, Cardiff, Wales, and completed postdoctoral research at Florida State University. It was while teaching Ecology at the University of the West Indies, Trinidad, that the idea for this book was conceived. Dr. Stiling's research interests include plant–insect relationships, parasite–host interactions, and biological control. He has published many scientific papers in journals such as *Ecology*, *Oikos*, and *Oecologia*. His current field research, supported by the National Science Foundation, focuses on insect communities on salt marsh plants.

Preface to the First Edition

WHO STARTED ECOLOGY?

Most authors, including the Oxford English Dictionary and the Encyclopedia Britannica, ascribe the term Ecology to Ernst Haeckel who, in 1866, defined it as "the comprehensive science of the relationship of the organism to the environment"—a useful definition even today. However, the first recorded usage was in a letter by Henry David Thoreau in 1858. These early uses of the term ecology seem oblique and Goodland (1875) argues convincingly that the Dane, Eugen Warming (1841–1924), should be regarded as the founder of the science of ecology because of his pioneering research in Brazil and because he wrote the first book on the subject in 1895 (Warming 1895).

WHAT IS ECOLOGY?

To most people today, ecology is associated with the broad problems of the human environment, especially pollution. To others, ecology is synonymous with conservation and saving the whales or the forests. Yet, ecology does not simply deal with pollution or conservation, it is related to the environment much as physics is to engineering. Ecology provides the scientific framework upon which conservation programs or pollution monitoring schemes can be set up. The scientific framework is often erected, however, not from studies of rare, exotic animals or studies of oil spills but from studies of invertebrates such as insects, and small, relatively unappealing plants because these best can be manipulated experimentally to test ecological theories. For example, it is rather difficult to experiment with blue whales or Florida panthers, of which there are relatively few. This book is, thus, peppered with studies of the teeming hordes of common life.

The biosphere is composed of some 1.8 metric tons of living tissue and covers the surface of the globe in a layer proportionately thinner than the skin of an apple. If all the material were evenly distributed, it would be less than 1 cm thick and weigh about 3.6 kg (Anderson 1981), but the Earth's biomass is not evenly distributed. It shows great variation, from about 45 kg in tropical forests to 0.003 kg in the oceans. Ecology is concerned with explaining this variation; it asks why plants and animals are found in certain areas and what controls their numbers. The study of ecology can be divided into two areas. Functional ecology asks how populations are maintained at a particular size and touches on behavior, competition, predation, and other contemporaneous factors. Historical ecology asks how populations have come to be this way and places great emphasis on biogeography (the study of global distribution patterns and shared characteristics), which presupposes a knowledge of continental drift and of evolution.

TEXT DEVELOPMENT

In 1983, I began teaching ecology to students in the Department of Zoology at the University of the West Indies, Trinidad. Most had little prior ecological background, so I started from scratch. I wanted to give the students a full overview of ecology and not specialize in one particular area; I needed to present an introductory ecology course. As previously noted, a full understanding of ecology requires some knowledge of historical ecology and, thus, of evolution, so, to begin, I introduced a little evolutionary ecology. Also, I wanted to include some ecology of animal behavior, a fascinating area and one enjoyed by most students. An ecology course should also encompass population biology, the regulation of plant and animal numbers, which is the core material of most texts and the area where most ecologists publish (Stiling 1994). Coverage of communities was also necessary as it is this area which is noted as of most interest to ecologists in surveys (Travis 1989). And finally, I thought there should be some reference to applied ecology. For most of these students, a knowledge of applied ecology would be essential in the real world to which they would soon belong. Having set this outline for my introductory course, I found that there was no textbook incorporating evolutionary ecology, behavioral ecology, population ecology, community ecology, and applied ecology. This book is an attempt to remedy that situation. It assumes knowledge of college-level biology, perhaps that offered by an introductory biology course in which some knowledge of genetics and heredity, physiological adaptation of plants and animals, and the diversity of life have been touched upon.

THEMES

This book has several main themes. First, it is broad in coverage. Few other ecology texts attempt as diverse a treatment in explaining the distribution and abundance of plants and animals. Take for example the distribution patterns of the polar bear. Why is it not found in the Antarctic? Clearly, climate and topography are not sufficient answers. For this species, a knowledge of evolutionary ecology is vital. For many other species, particularly those with good dispersal abilities, such as plants, physiological factors are the main constraints on observed distribution patterns. Within these distribution patterns, the abundance of species can be affected by food supply, competitors, predators, and parasites and, for animals, territorial behavior. Thus, a sound knowledge of population ecology is essential. Ultimately population fluctuations may be influenced by higher-order community interactions—hence, the value of examining ecological processes at these large spatial scales. Finally, so many ecological processes are impacted by people, especially in these times of exploding population growth, that it is worthwhile to examine ecological phenomena as they are affected by humans—applied ecology. Breadth, of course, has its drawbacks. By combining many elements into an introductory course, the text could become overly long. I have resisted this temptation by presenting ideas as succinctly as possible. The result is, I hope, a streamlined introductory ecology text.

A second main theme of this book is to present both sides of an argument. Many texts are content to tell a "just so" story. This is often true when ecological processes are modeled. There is a great temptation either to present a model and then the evidence to back it up or to spend a long time concocting a model to fit available data. It is very easy to present an ecological principle with a "happy ending," that is, a nice tidy explanation with no loose ends, that appeals to the student and is intellectually satisfying. Unfortunately, as most field ecologists know, the actual data are rarely neat and often fit no clearcut hypothesis. Even if the data do fit a hypothesis, the next set of data taken in another system is just as likely to show the opposite trend. To combat this, I have tried, wherever possible, to present a variety of evidence both for and against proposed theories.

CHAPTER FORMAT

It is difficult, in such a wide-ranging book as this, to stick to one particular format for each chapter. There are, however, some generalities of approach that are worth bringing out. In each chapter, the ideas and theory are discussed first, then some examples follow, both for and against the proposed hypotheses. I have tried to keep these examples to a minimum. Often, modern examples are used but sometimes older work is referred to. There are many older pieces of work that will forever remain standards. In the field of competition theory, for example, the displacement of one species of parasitic *Aphytis* wasp by another in Southern California will probably forever remain a classic example of competitive displacement in the field. Nevertheless, references are kept as updated as possible; over 12% are from the 1990s. This is, therefore, an unusually current treatment of ecology. Following the examples, I discuss any recent overviews of the subject. Ultimately, one is swayed either for or against a theory by the weight of the evidence. I cannot present all the pertinent data for and against one theory in this book, but I can refer the reader to the research papers that do. For example, in discussing the frequency of density dependent parasitism (Chapter 11), I point out that two independent reviews (Stiling 1987; Walde and Murdoch 1988) have shown that in nature density dependence does not occur very frequently despite the fact that many ecologists have based much of their work on modeling density dependence. Similar reviews are referred to in the section on competition (Connell 1983; Schoener 1983; Denno et al. 1995) and predation (Sih et al. 1985). It is my hope that in the not-too-distant future all subject areas of ecology will be methodically reviewed in this way so that ecologists will no longer be content to pull contrasting examples out of a hat and that there will be a review that will show a preponderance of the evidence going one way or the other.

CHAPTER ELEMENTS

In determining the actual layout of each chapter, I have relied heavily on the use of tables, figures, and photographs to present the evidence. As Connor and Simberloff (1979a) noted, "You can't falsify ecological hypotheses without data." I personally chose each table, figure, and photograph that is used in the book (and had to write all the letters of permission to use them!). Each piece of illustrative material is directly related to a point raised in the text. To maintain the brevity of style, however, the text does not usually go over the same ground. Each table, figure, or photograph is intended to be self-explanatory. Other more superficial learning tools, such as boxed essays and asides, are absent. Material that could be presented in this way is simply integrated into the text. I have tried to lessen the effects of ecological jargon by providing a glossary. Terms that are boldface, plus some that are not, are defined at the end of the book. Though the book tries to be brief and not burden the student with unnecessary baggage, which they would have to sift through with a highlighter, it is well referenced so that the interested reader can always find where to read further on a subject. Despite its size, there are more references in this text than in many of its competitors.

KEY CONTENT

There is a necessary tradeoff between classical material and recent developments. In ecology, subjects such as biodiversity, conservation, restoration, bioengineering, acid rain, and global warming get much of the press. These are all important issues. But it is worth remembering that predicting the effects of such things is often based on more traditional disciplines. Thus, conservation ecology relies heavily on population ecology. To predict the effects of genetically engineered organisms, many experts have used as analogs the results of releasing exotic species into novel environments. Physiological ecology can best give us the likely answers to questions of how the distribution patterns of species will change in the event of climatic alterations. This book attempts to integrate new concepts with new and older theory.

It has often been said that biology only makes sense in the context of evolution. I begin this book with a treatment of evolutionary ecology, the end point being to discuss the reasons for extinction of plants and animals today. This is followed by Section Three, Population Biology, in which I discuss the multitude of effects of the environment, competition, predation, herbivory, parasitism, and other factors on the abundance of plants and animals, and tie these together by comparing their effects in the final chapter entitled "The Causes of Population Change." Section Four, Community Ecology, discusses the integration of populations into communities, the units in which they occur in nature. Things such as species diversity, diversity gradients, stability, succession, and biogeography are discussed here. In Section Five, Ecosystems Ecology, I explain the flow of energy and nutrients through communities and the assemblage of trophic links in ecosystems. With this background established, we are in a position to discuss the impacts of humans. The last section, Applied Ecology, documents the main effects of people; habitat destruction, exploitation of wildlife for its own sake, pollution, and the introduction of exotic organisms.

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Finally, I should like to offer my sincere appreciation to Anne Thistle for a meticulous job of typing and editing this book and for making me look much better grammatically. Heartfelt thanks to Sharon Strauss, University of Illinois, who had the fortitude to read the entire thing. My editors, Betty O'Bryant at Technical Texts and David Brake at Prentice Hall, provided many helpful suggestions. Students at the University of West Indies, Trinidad, and at the University of South Florida have been quick to point out any inconsistencies. However, I would be pleased to hear about errors in fact or interpretation, omission of material, further examples, or other relevant ideas.

Preface to the Second Edition

The changes for this second edition have been quite extensive—there are 62 new figures and tables and over 300 new references. New ideas, new concepts and new examples have been included in the text to keep the book current. However, this revision is not just an "in with the new, out with the old" exercise. Many existing sections have been thoroughly reworked for clarity. The annoying little errors that are often present in first editions, such as typographical errors or mistakes in equations, have been fixed. But again, this edition is not simply about fixing mistakes. It incorporates major conceptual changes. Although the text still has an "applied ecology" section, I have made a strong effort to integrate much "applied" material into the entire text. Thus, there is coverage of global warming in Chapter 5, conservation biology in Chapters 2 and 3, biodiversity in Chapter 14, and restoration ecology in Chapter 19.

As regards specific sections, among the first and most important changes are to be found in Section Two, Evolutionary and Behavioral Ecology. Both evolution and behavior are important in the study of ecology. What I have done in the second edition is to make this material more like evolutionary and behavioral ecology and less like straight evolution and behavior. For example, the seemingly simple species concept is shown to be far from simple and the relevance of this to conservation biology underscored.

Many chapters in Section Three, Population Biology, have been updated. The chapter on population growth, Chapter 6, has been thoroughly stripped down and rewritten and now includes material on time-lags and chaos. The biggest change of all in Section Three is in the last chapter, Chapter 12, which gives a broader synthesis of the causes of population change and population regulation. Factorial experiments are introduced as a good way to compare the strength of mortality factors. Population equilibrium and the idea of metapopulations are introduced to students. Density vagueness and the CV^2 rule are contrasted with ideas about density dependence. The HSS, OF and MS models are compared, top-down and bottom-up effects are contrasted and indirect effects are introduced in their own subsection.

The fourth part of the book, Community Ecology, has been expanded to include material on rarefaction, cardinal versus ordinal indices and rank-abundance diagrams. The material on ecosystems has been lengthened and given more emphasis in its own two-chapter section. Biogeochemical cycles are given increased coverage with new subsections on the phosphorus and carbon cycles.

Most of the environmental problems that exist in today's world can be traced to a still increasing human population. It is for this reason that, in Section Six, Applied Ecology, the topic of human population growth has been dealt with in more detail. Like Section Two, this section has been thoroughly stripped down and rewritten. The discussion on design of nature preserves now incorporates the concept of Minimum Viable Population (MVP) and prevention of poaching, as well as more traditional areas like the SLOSS debate. There is now a new subsection entitled Restoration Ecology. Students enjoy talking about restoration ecology because many of them envisage careers in this area.

The following users of the first edition provided critiques which have proven invaluable in the preparation of the second edition: Gary K. Clambey, North Dakota State University; Daniel F. Doak, University of California-Santa Cruz; Kristina A. Ernest, Central Washington University; Margaret H. Fusari, University of California-Santa Cruz; Nicholas J. Gotelli, University of Vermont; Jeffrey R. Lucas, Purdue University; Peter Smallwood, Bryn Mawr College, Pennsylvania; Karen Olmstead, University of South Dakota; and Roy A. Stein and Alison Snow, Ohio State University. My new editor, Sheri Snavely, was instrumental in upgrading the production values for the book, including a two-color format and color photographic inserts. The whole feel of the book benefited from her efforts. I particularly appreciate the efforts of Electronic Publishing Services Inc. in the copyediting, proofreading, photo research, and production of the book. And finally, Jacqui Stiling deserves special mention—without her constant efforts and computer expertise this second edition would not have been possible.

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