Preface

The accelerating pace of discovery makes the teaching of a dynamic scientific discipline such as ecology very challenging. The challenge to ecology instructors and their students is made greater by the relevance of ecology to the pressing environmental problems that threaten ecological systems at every level. As we attempt to educate students to understand and design solutions to those problems, every facet of ecology is relevant. Therefore, ideally, an introduction to ecology should include the foundations to all of its major subdisciplines. Including such breadth, and developing it to sufficient depth, is difficult. However, careful organization and a conceptual approach can ease the task.

Introductory Audience

I have written this book for students taking their first undergraduate course in ecology. I have assumed that students in this one-semester course have some knowledge of basic chemistry and mathematics and that they have had a course in general biology that included introductions to physiology, biological diversity, and evolution.

> *"I receive positive feedback about the text from my students. During or after the course, some students majoring in other fields have expressed an interest in switching to ecology as a major, and I believe the text contributes toward that interest."*
>
> —Carolyn Meyer
> *University of Wyoming*

Unique Approach

In an address at the 1991 meeting of the Ecological Society of America in San Antonio, Texas, eminent ecologist Paul Risser challenged ecology instructors to focus their attention on the major concepts of the field. If we subdivide a large and dynamic subject, such as ecology, too finely, we cannot cover it in one or two academic terms. Risser proposed that by focusing on major concepts, however, we may provide students with a robust framework of the discipline upon which they can build.

This book attempts to address Risser's challenge. **Each chapter is organized around two to five major concepts, presenting the student with a manageable and memorable synthesis of the subject.** I have found that while beginning ecology students can absorb a few central concepts well, they can easily get lost in a sea of details. Each concept is supported by discussions that provide evidence for the concept and introduce students to the research approaches used in the various areas of ecology. Wherever possible, the original research and the scientists who did the research are presented. Allowing the scientists who created this field to emerge from the background and lead students through the discipline breathes life into the subject and helps students retain information.

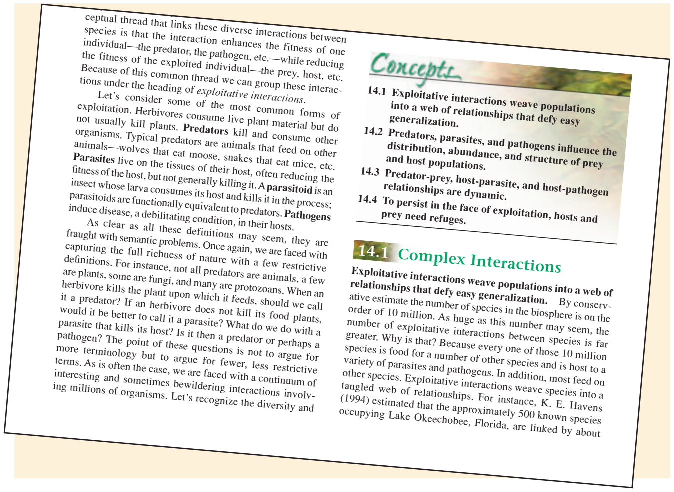
> *"What primarily motivated me to adopt* Ecology: Concepts and Applications *is the way the author emphasizes a few key ecological concepts in each chapter and then uses relevant studies to demonstrate how scientists have "discovered" these concepts. I find this emphasis on concepts and the science behind them to be a refreshing change from the typical textbook that tends to present the science of ecology as a rather dull collection of facts. I feel that the students who read this text will come away with a better understanding not only of ecology, but also of the method of doing science."*
>
> —Tim Maret
> *Shippensburg University*

New to This Edition

All 23 chapters of the book have been revised following the suggestions of numerous reviewers. An attempt was made to address reviewers' concerns, to update material where needed, add missing perspectives, correct errors, and generally freshen and streamline the treatment. Suggested readings have been shortened and updated, drawing mainly from literature published since the publication of the third edition.

The presentation has been reformatted to help students orient to the flow of information in each chapter. The concepts in each chapter are now numbered both in the first listing of chapter concepts and at the beginning of each section in which concepts are discussed. The concept numbers are repeated in the concept review questions that conclude each concept section. Thus the beginning and end of all concepts are signaled clearly for the student. Each "Investigating the Evidence" boxed discussion is also given the number of the chapter in which it appears, again as a locator for the student.

Over 240 study questions have been added throughout the text to help students review the major concepts. The "Concept


ceptual thread that links these diverse interactions between species is that the interaction enhances the fitness of one individual—the predator, the pathogen, etc.—while reducing the fitness of the exploited individual—the prey, host, etc. Because of this common thread we can group these interactions under the heading of *exploitative interactions.*

Let's consider some of the most common forms of exploitation. Herbivores consume live plant material but do not usually kill plants. **Predators** kill and consume other organisms. Typical predators are animals that feed on other animals—wolves that eat moose, snakes that eat mice, etc. **Parasites** live on the tissues of their host, often reducing the fitness of the host, but not generally killing it. A **parasitoid** is an insect whose larva consumes its host and kills it in the process; parasitoids are functionally equivalent to predators. **Pathogens** induce disease, a debilitating condition, in their hosts.

As clear as all these definitions may seem, they are fraught with semantic problems. Once again, we are faced with capturing the full richness of nature with a few restrictive definitions. For instance, not all predators are animals, a few are plants, some are fungi, and many are protozoans. When an herbivore kills the plant upon which it feeds, should we call it a predator? If an herbivore does not kill its food plants, would it be better to call it a parasite? What do we do with a parasite that kills its host? Is it then a predator or perhaps a pathogen? The point of these questions is not to argue for more terminology but to argue for fewer, less restrictive terms. As is often the case, we are faced with a continuum of interesting and sometimes bewildering interactions involving millions of organisms. Let's recognize the diversity and

Concepts

14.1 Exploitative interactions weave populations into a web of relationships that defy easy generalization.
14.2 Predators, parasites, and pathogens influence the distribution, abundance, and structure of prey and host populations.
14.3 Predator-prey, host-parasite, and host-pathogen relationships are dynamic.
14.4 To persist in the face of exploitation, hosts and prey need refuges.

14.1 Complex Interactions

Exploitative interactions weave populations into a web of relationships that defy easy generalization. By conservative estimate the number of species in the biosphere is on the order of 10 million. As huge as this number may seem, the number of exploitative interactions between species is far greater. Why is that? Because every one of those 10 million species is food for a number of other species and is host to a variety of parasites and pathogens. In addition, most feed on other species. Exploitative interactions weave species into a tangled web of relationships. For instance, K. E. Havens (1994) estimated that the approximately 500 known species occupying Lake Okeechobee, Florida, are linked by about

Review" questions that conclude each concept discussion are designed to help students think critically about content and to encourage them to reflect on the design of research projects and on the thinking of researchers. "Investigating the Evidence" boxed discussions include questions called "Critiquing the Evidence," which are intended to explore some of the details of the statistics and study design topics presented.

Two new appendixes provide the answers to the more than 240 "Concept Review" and "Critiquing the Evidence" questions.

A list of key terms at the end of each chapter alerts students to new vocabulary as it is introduced.

Organized Around Key Concepts

An evolutionary perspective forms the foundation of the entire textbook, as it is needed to support understanding of major concepts. The textbook begins with a brief introduction to the nature and history of the discipline of ecology, followed by section I, which includes two chapters on natural history—life on land and life in water. Sections II through VI build a hierarchical perspective through the traditional subdisciplines of ecology: section II concerns the ecology of individuals; section III focuses on population ecology; section IV presents the ecology of interactions; section V summarizes community and ecosystem ecology; and finally, section VI discusses large-scale ecology and includes chapters on landscape, geographic, and global ecology. These topics were first introduced in section I within a natural history context. In summary, the book begins with the natural history of the planet, considers portions of the whole in the middle chapters, and ends with another perspective of the entire planet in the concluding chapter.

Significant Changes

In ***chapter 3,*** the zebra mussel information was updated, and the biome descriptions were edited to make them more concise.

In ***chapter 6,*** I added material on the evolution, diversity, and significance of C_4 plants, and cross-referenced materials to chapters 18 (Liebig's law), 19 (nutrient cycling), and 23 (atmospheric CO_2 increase).

I introduced Hamilton's rule in ***chapter 7,*** converted a former Application to a Concept focused on evolution of eusociality and shortened for better coherence, and added a new Application on the utility of behavioral ecology in conservation.

In ***chapter 9,*** the discussion of distributions was divided into two concepts, one focused on small-scale patterns, and the other one focused on large-scale patterns. Metapopulation discussion has been moved from chapter 9 of the third edition to chapter 10.

In ***chapter 11,*** the whooping crane population growth record has been updated, as well as all the human population statistics.

In ***chapter 13,*** I explained the introductory story about root competition in more detail, rewrote two concepts to better reflect material and to be more concise, and revised and shortened the flour beetle competition experiments discussion.

In ***chapter 23,*** I updated information on the ozone hole, changed the concluding section on "The Future" to underscore the magnitude and rapidity of current global change, especially existing and predicted environmental and ecological responses to global warming. I updated the information on the U.S. LTER Network and the International LTER network, including an update of the map of the U.S. LTER network.

Features Designed with the Student in Mind

The features of this textbook are unique and were carefully planned to enhance the students' comprehension of ecology. All chapters beyond the introductory chapter 1 are based on a distinctive learning system, featuring the following key components:

Introduction: The introduction to each chapter presents the student with the flavor of the subject and important background information. Some introductions include historical events related to the subject; others present an example of an ecological process. All attempt to engage students and draw them into the discussion that follows.

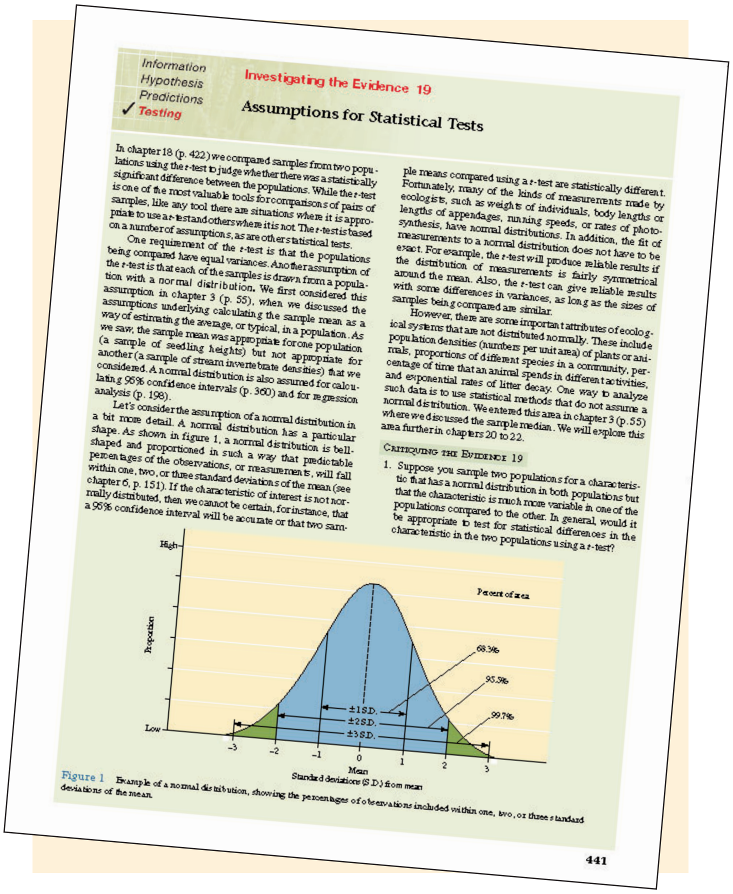
Concepts: The goal of this book is to build a foundation of ecological knowledge around key concepts. These key concepts are listed after the chapter introduction to alert the student to the major topics to follow, and to provide a place where the student can find a list of the important points of each chapter. The sections in which concepts are discussed reinforce concepts with a focus on published studies. This case-study approach supports the concepts with evidence, and introduces students to the methods and people that have created the discipline of ecology.

Applications: Many undergraduate students want to know how abstract ideas and general relationships can be applied to the ecological problems facing us all. They are concerned with the practical side of ecology and want to know more about the tools of science. Including a few applications in each chapter motivates students to learn more of the underlying principles of ecology. In addition, it seems that environmental problems are now so numerous and so pressing that they have erased a once easy distinction between general and applied ecology.

"The idea of Applications sections in the chapter is excellent."

—Frank S. Gilliam
Marshall University

"Investigating the Evidence" Boxes: These important readings offer "mini-lessons" on the scientific method, emphasizing statistics and study design. They are intended to present a broad outline of the process of science, while also providing step-by-step explanation. The series of boxes begins in chapter 1 with an overview of the scientific method, which provides a conceptual context for more specific material in the next 21 chapters. The last reading wraps up the series with a discussion on electronic literature searches.


Information
Hypothesis
Predictions
✓ Testing

Investigating the Evidence 19

Assumptions for Statistical Tests

In chapter 18 (p. 422) we compared samples from two populations using the *t*-test to judge whether there was a statistically significant difference between the populations. While the *t*-test is one of the most valuable tools for comparisons of pairs of samples, like any tool there are situations where it is appropriate to use a *t*-test and others where it is not. The *t*-test is based on a number of assumptions, as are other statistical tests.

One requirement of the *t*-test is that the populations being compared have equal variances. Another assumption of the *t*-test is that each of the samples is drawn from a population with a normal distribution. We first considered this assumption in chapter 3 (p. 55), when we discussed the assumptions underlying calculating the sample mean as a way of estimating the average, or typical, in a population. As we saw, the sample mean was appropriate for one population (a sample of seedling heights) but not appropriate for another (a sample of stream invertebrate densities) that we considered. A normal distribution is also assumed for calculating 95% confidence intervals (p. 360) and for regression analysis (p. 198).

Let's consider the assumption of a normal distribution in a bit more detail. A normal distribution has a particular shape. As shown in figure 1, a normal distribution is bell-shaped and proportioned in such a way that predictable percentages of the observations, or measurements, will fall within one, two, or three standard deviations of the mean (see chapter 6, p. 151). If the characteristic of interest is not normally distributed, then we cannot be certain, for instance, that a 95% confidence interval will be accurate or that two sample means compared using a *t*-test are statistically different.

Fortunately, many of the kinds of measurements made by ecologists, such as weights of individuals, body lengths or lengths of appendages, running speeds, or rates of photosynthesis, have normal distributions. In addition, the fit of measurements to a normal distribution does not have to be exact. For example, the *t*-test will produce reliable results if the distribution of measurements is fairly symmetrical around the mean. Also, the *t*-test can give reliable results with some differences in variances, as long as the sizes of samples being compared are similar.

However, there are some important attributes of ecological systems that are not distributed normally. These include population densities (numbers per unit area) of plants or animals, proportions of different species in a community, percentage of time that an animal spends in different activities, and exponential rates of litter decay. One way to analyze such data is to use statistical methods that do not assume a normal distribution. We entered this area in chapter 3 (p. 55) where we discussed the sample median. We will explore this area further in chapters 20 to 22.

Critiquing the Evidence 19

1. Suppose you sample two populations for a characteristic that has a normal distribution in both populations but that the characteristic is much more variable in one of the populations compared to the other. In general, would it be appropriate to test for statistical differences in the characteristic in the two populations using a *t*-test?

Figure 1 Example of a normal distribution, showing the percentages of observations included within one, two, or three standard deviations of the mean.

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"What I really like are the Investigating the Evidence (boxes) scattered through the chapters. This is an absolutely brilliant way to encourage quantification especially if there is no lab associated with the course."

—Peter E. Busher
Boston University


Chapter 14 Exploitative Interactions: Predation, Herbivory, Parasitism, and Disease 343

Applications

Using Predators to Control a Parasite

Parasitic diseases afflict approximately 600 million people across the planet, particularly in tropical and subtropical countries. Despite intensive efforts at control, many parasitic diseases are spreading and the number of cases appears to be increasing. A key factor in this increase appears to be human population growth, which puts additional pressure on sanitation and health care systems and increases the number of hosts for human parasites. The leading parasitic disease in humans is malaria, which is transmitted to humans by mosquitoes and infects an estimated 250 million people. The second most prevalent parasitic disease is schistosomiasis, which infects approximately 200 million people. Schistosomiasis is a debilitating infection caused by blood flukes of the genus *Schistosoma*. Infections by this parasite are particularly debilitating to children. The scope and intensity of infections by *Schistosoma* and other parasites challenge the world health community to develop systems for their control. However, the problem of control is essentially an ecological one and therefore complex.

Much of this complexity is due to the life cycle of the parasite (fig. 14.29). *Schistosoma* spends its larval phase as a parasite in aquatic snails and its adult phase in humans. The *cercariae*, the stage of *Schistosoma* that infects humans, are released by snails into the water. Cercariae penetrate the skin of humans in streams, lakes, or ponds containing infected snails. Some *Schistosoma* infect the human digestive tract while others infect the urinary tract. Humans that either urinate or defecate in water complete the parasite's life cycle by facilitating the infection of snails.

Schistosomiasis can now be treated with a variety of drugs. However, treated patients are often reinfected. Consequently, schistosomiasis control programs that rely solely on treatment of infected individuals cannot control the spread of infection. Effective control must also include the populations of snails that serve as intermediate hosts. Methods of snail control have included applications of chemicals that kill snails, introduction of other snails that competitively displace the snail species that serve as intermediate hosts for *Schistosoma*, or, increasingly, using predators to control snail populations. This work draws upon Concept 14.2 of chapter 14: predators, parasites, and pathogens influence the distribution, abundance, and structure of prey and host populations.

Scientists in several East African countries are researching the potential of a variety of predators to control the host snails infected by *Schistosoma*. One of those countries is Kenya. Kenya's population includes 1 to 2 million people infected with *Schistosoma*. Health officials are concerned that the number of cases may increase due to increased pollution of freshwater environments by untreated sewage and increased construction of dams and irrigation systems, which favor the growth of snail populations. In the face of these threats, Kenyan health officials are developing a comprehensive, multifaceted plan for control of schistosomiasis. One of the elements in their plan is to use predators to control the parasite's host snails.

One of the predators being tested for its effectiveness at snail control is the crayfish *Procambarus clarkii*, which is native to North America. *Procambarus* was introduced into Kenya during the 1970s. Health officials became interested in the potential of the crayfish to control snail populations when snail surveys showed that habitats with *Procambarus* lacked host snails. However, because *Procambarus* is not native to Kenya, ecologists and health officials are proceeding

Figure 14.29 The life cycle of *Schistosoma*.

Illustrations: A great deal of effort has been put into the development of illustrations, both photographs and line art. The goal has been to create more effective pedagogical tools through skillful design and use of color, and to rearrange the traditional presentation of information in figures and captions. Much explanatory material is located within the illustrations, providing students with key information where they need it most.

"I love the boxes in the illustrations! I think they facilitate both the reading and comprehension for the students. I think this style is the most helpful with the graphs and charts."

—Tatiana Roth
Coppin State College

End-of-Chapter Material:

- ***Summary*** The chapter summary reviews the main points of the content. The concepts around which each chapter is organized are boldfaced and redefined in the summary to emphasize once again the main points of the chapter.

- ***Key Terms***
- ***Review Questions*** The review questions are designed to help students think more deeply about each concept and to reflect on alternative views. They also provide a place to fill in any remaining gaps in the information presented and take students beyond the foundation established in the main body of the chapter.
- ***Suggested Readings*** Each chapter ends with a list of suggested readings. Though all of the readings offer the student coverage beyond the chapter content, they have been chosen to serve a variety of purposes. Some are books that provide a broad overview; others are papers that trace the development of particular topics or controversies in ecology. I have provided a brief description and rationale for each.

End-of-Book Material:

- ***Appendixes*** Three appendixes, "Statistical Tables," "Answers to Concept Review Questions," and "Answers to Critiquing the Evidence," are available to the student for reference and as study aids.
- ***Glossary***
- ***References*** References are an important part of any scientific work. However, many undergraduates are distracted by a large number of references within the text. One of the goals of a general ecology course should be to introduce these students to the primary literature without burying them in citations. The number of citations has been reduced to those necessary to support detailed discussions of particular research projects.
- ***Index***

"This text is extraordinarily well integrated. The recurring emphasis of how the scientific method and process are used within the methods used in each case study is very well done."

—Thomas Pliske
Florida International University

Teaching and Learning Supplements

McGraw-Hill offers various tools and technology products to support *Ecology: Concepts and Applications*. Students can order supplemental study materials by contacting their local bookstore or by calling 800-262-4729. Instructors can obtain teaching aids by calling the Customer Service Department at 800-338-3987, visiting the McGraw-Hill website at www.mhhe.com, or by contacting their local McGraw-Hill sales representative.

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- Class activities
- PowerPoint lecture presentations
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- **Color Art** Full-color digital files of ALL illustrations in the text can be readily incorporated into lecture presentations, exams, or custom-made classroom materials. These include all of the 3-D realistic art found in this edition, representing some of the most important concepts in ecology.
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- **Tables** Every table that appears in the text is provided in electronic format.

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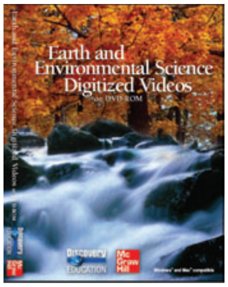
- **PowerPoint Lecture Outlines** Ready-made presentations that combine art and photos and lecture notes are provided for each of the 23 chapters of the text. These outlines can be used as they are, or tailored to reflect your preferred lecture topics and sequences.
- **PowerPoint Slides** For instructors who prefer to create their lectures from scratch, all illustrations, photos, and tables are preinserted by chapter into blank PowerPoint slides for convenience.



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- Practice quizzing
- Hyperlinks on chapter topics
- Links to professional, educational, and governmental organizations
- Animations
- Guide to electronic research
- Regional perspectives (case studies)
- Lab exercises
- Ecology/environmental science issues world map
- Periodic table
- Key term flashcards
- Career information

***Field and Lab Methods for General Ecology,* Fourth Edition by Brower et al. (ISBN: 978-0-697-24358-4; MHID: 0-69-724358-3)**

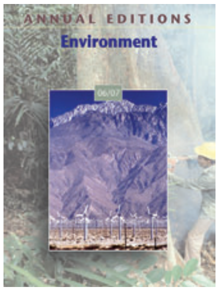
This introductory ecology lab manual focuses on the process of collecting, recording, and analyzing data, and equips students with the tools they need to function in more advanced science courses. It reflects the most current techniques for data gathering so that students can obtain the most accurate samples. Balanced coverage of plant, animal, and physical elements offers a diverse range of exercises. The lab manual includes an exercise on writing research reports.

***General Ecology Laboratory Manual,* Eighth Edition by Cox (ISBN: 978-0-07-290974-6; MHID: 0-07-290974-9)**

Designed for juniors and seniors, this one-semester laboratory manual is based on mathematical statistics. Author George Cox begins with exercises covering library research, designing an ecological study, and other introductory concepts. He then proceeds to an examination of specific types of measurement and an analysis of various aspects of ecology. Many of these laboratories are tied to current, commercially available computer programs and software packages.

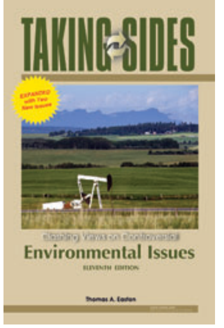
***Exploring Environmental Science with GIS* by Stewart, Cunningham, Schneiderman, and Gold (ISBN: 978-0-07-297564-2; MHID: 0-07-297564-4)**

This short book provides exercises for students and instructors who are new to GIS, but are familiar with the Windows operating system. The exercises focus on improving analytical skills, understanding spatial relationships, and understanding the nature and structure of environmental data. Because the software used is distributed free of charge, this text is appropriate for courses and schools that are not yet ready to commit to the expense and time involved in acquiring other GIS packages.



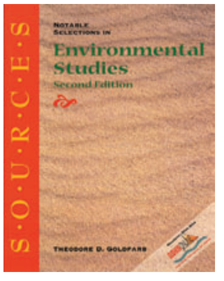
***Annual Editions: Environment 06/07* by Allen (ISBN: 978-0-07-351542-7; MHID: 0-07-351542-6)**

This twenty-fifth edition is a compilation of current articles from the best of the public press. The selections explore the global environment, the world's population, energy, the biosphere, natural resources, and pollutions.



***Taking Sides: Clashing Views on Controversial Environmental Issues,* Expanded Eleventh Edition by Easton (ISBN: 978-0-07-351441-3; MHID: 0-07-351441-1)**

This book represents the arguments of leading environmentalists, scientists, and policymakers. The issues reflect a variety of viewpoints and are staged as "pro" and "con" debates. Issues are organized around four core areas: general philosophical and political issues, the environment and technology, disposing of wastes, and the environment and the future.



***Sources: Notable Selections in Environmental Studies,* Second Edition by Goldfarb (ISBN: 978-0-07-303186-6; MHID: 0-07-303186-0)**

This volume brings together primary source selections of enduring intellectual value—classic articles, book excerpts, and research studies—that have shaped environmental studies and our contemporary understanding of it. The book includes carefully edited selections from the works of the most distinguished environmental observers, past and present. Selections are organized topically around the following major areas of study: energy, environmental degradation, population issues and the environment, human health and the environment, and environment and society.

***Student Atlas of Environmental Issues,* by Allen (ISBN: 978-0-69-736520-0; MHID: 0-69-736520-4)**

This atlas is an invaluable pedagogical tool for exploring the human impact on the air, waters, biosphere, and land in every major world region. This informative resource provides a unique combination of maps and data that help students understand the dimensions of the world's environmental problems and the geographical basis of these problems.

Acknowledgments

A complete list of the people who have helped me with this project would be impossibly long. However, during the development of this fourth edition, several colleagues freely shared their ideas and expertise, reviewed new sections, and offered the encouragement a project like this needs to keep it going: Eric Charnov, Scott Collins, John Craig, Cliff Crawford, Cliff Dahm, Tim Lowrey, Randy Thornhill, Eric Toolson, and Robert Waide. I wish to offer special thanks to professor Jianguo Wu for his time and patience in helping me improve the historical and conceptual framework for the chapter on landscape ecology. In addition, I am indebted to the many student readers of earlier editions who have helped by contacting me with questions and suggestions for improvements.

I also wish to acknowledge the skillful guidance throughout the publishing process given by many professionals associated with McGraw-Hill during this project, including Marge Kemp, Brian Loehr, Joan Weber, Tami Petsche, Dan Wallace, Laurie Janssen, Melissa Leick, Judi David, Gloria Schiesl, Carrie Burger, and Laura Fuller.

Finally, I wish to thank all my family for support given throughout the project, especially Mary Ann Esparza, Dan Esparza, Hani Molles, Anders Molles, Mary Anne Nelson, and Misha.

I gratefully acknowledge the many reviewers who, over the course of the last several revisions, have given of their time and expertise to help this textbook evolve to its present fourth edition. Their depth and breadth of knowledge and experience, both as researchers and teachers, are humbling. I honestly could not have done it without them.

Reviewers for the Fourth Edition

John M. Anderies *Arizona State University*
Eric M. Anderson *University of Wisconsin–Stevens Point*
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