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

A Focused 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 updated, drawing mainly from literature published since the publication of the fourth edition.

The introduction now links the historical foundations of ecology with developing frontiers. Emphasis is placed on how new tools, such as stable isotope analysis and canopy access cranes, provide more powerful ways of investigating ecological systems, as we explore and attempt to sustain biodiversity in the face of global climate change and other environmental pressures.

The evolutionary foundation for the book has been strengthened. The chapter on population genetics and natural selection has been moved from eighth position, in section III, to fourth, in section I. Section I is now titled *Natural History and Evolution.* Moving evolution to this point in the text sets all the material to follow in a stronger evolutionary

framework. This is particularly significant to section II, which is retitled as *Adaptations to the Environment.*

The overall conceptual foundation of the text has been enriched. New concepts presented include the principle of allocation, apparent competition, indirect mutualism, and the ecology of fear.

The treatment of nutrient cycling has been improved. The nutrient cycling presentation now appears under its own umbrella concept and is buttressed by the addition of central concepts, including nutrient sinks, sources, fluxes, and pools, which are critical for understanding contemporary issues related to the buildup of atmospheric carbon dioxide.

Lessons learned through the Investigating the Evidence boxes enrich the graphical presentation. Confidence intervals and standard error bars are added to selected graphs once the statistical concepts are introduced in section IV.

New supplementary materials have been placed online. Suggested readings, answers to Concept Review questions, and answers to Critiquing the Evidence questions are now online. In addition, examples cut from the fourth edition are also available online.

New chapter opener photos, related to chapter content, have been added to enrich the visual presentation of ecology.

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 and a chapter on population genetics and natural selection. Sections II through VI build a hierarchical perspective through the traditional subdisciplines of ecology: section II concerns adaptations to the environment; 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 2,*** the maps of individual biomes are now supplemented by a global map of all the terrestrial biomes that appears on the inside back cover of the text.

In ***chapter 4,*** the treatment of evolution by natural selection is extended by presenting Darwin's conceptual connection of artificial selection to natural selection and discussing the significance of evolution to agriculture, including genetic engineering and genetically modified organisms.

In ***chapter 5,*** the principle of allocation and the concept of tradeoffs are elaborated, improving the foundation for all subsequent discussions of environmental adaptations.

In ***chapter 7,*** the trophic diversity of life is underscored by presenting the ecology of photosynthetic autotrophs, chemosynthetic autotrophs, and heterotrophs under separate concepts. Photorespiration is also presented and tied to the evolution of alternative photosynthetic pathways.

In ***chapter 9,*** the niche concept is moved up earlier in the text and tied to patterns of distribution.

In ***chapter 13,*** the niche concept is revisited and connected to the concept of competitive exclusion.

In ***chapter 14,*** the ecology of fear is discussed within the context of refuges and its significance presented within the context of wolf restoration in Yellowstone National Park. The discussion foreshadows trophic cascades, which appear in chapter 18.

In ***chapter 15,*** the material on mycorrhizae is updated and improved by presenting the functional equilibrium model for allocation of energy by plants.

In ***chapter 16,*** the discussion of disturbance is extended to include the extreme levels of disturbance wrought by humans and points out how these levels of disturbance tie into the predictions of the intermediate disturbance hypothesis. The sampling discussion in Investigating the Evidence is tied to the canopy crane research introduced in chapter 1.

In ***chapter 17,*** indirect interactions, including indirect commensalism and apparent competition, are introduced under a new concept and developed both with text and new art work.

In ***chapter 18,*** trophic cascades are presented under the conceptual umbrella of indirect interactions, which were introduced in the previous chapter.

In ***chapter 19,*** nutrient cycles are more carefully presented within an enriched conceptual context and tied to current environmental concerns about the buildup of atmospheric carbon dioxide.

In ***chapter 21,*** edge effects and ecotones are included to better define landscape structure for students and to prepare for material on habitat fragmentation in chapter 23.

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.

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

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.

"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 15 Mutualism 353

budget that is invested in extrafloral nectaries and nectar should be low. This means that plants living on a tight energy budget, for example, plants living in a shady forest understory, should be less likely to invest in attracting ants than those living in full sun. Higher benefits result from (1) a high probability of attracting ants, that is, high p; (2) a high potential for herbivory, H; (3) low effectiveness of alternative defenses, low D; and (4) highly effective ant defense, high A.

The task for ecologists is to determine how well these requirements of the model match values of these variables in nature.

Concept 15.1.2

2. Suppose you discover a mutant form of *Helianthella quinquenervis* that does not produce extrafloral nectaries. What does Keller's theory predict concerning the relative fitness of these mutant plants and the typical ones that produce extrafloral nectaries?
2. According to Keller's theory, under what general conditions would the mutant *Helianthella quinquenervis*, lacking extrafloral nectaries, increase in frequency in a population and displace the typical plants that produce extrafloral nectaries?

Applications

Mutualism and Humans

Mutualism has been important in the lives and livelihood of humans for a long time. Historically, much of agriculture has depended upon mutualistic associations between species and much of agricultural management has been aimed at enhancing mutualisms, such as nitrogen fixation, mycorrhizae, and pollinators to improve crop production. Agriculture itself has been viewed as a mutualistic relationship between humans and crop and livestock species. However, there may be some qualitative differences between agriculture as it has been generally practiced and mutualisms among other species. How much of agriculture is pure exploitation and how much is truly mutualistic remains an open question.

There is, however, at least one human mutualism that fits comfortably among the earlier discussion in chapter 15, a mutualism involving communication between humans and wild species with clear benefit to both. This mutualism joins the traditional honey gatherers of Africa with the greater honeyguide, *Indicator indicator* (Fig. 15.22). Honey gathering has long been an important aspect of African culture, important enough that there are scenes of honey gathering on rock art painted over 20,000 years ago (Isack and Reyer 1989). No one knows how long human have gathered honey in Africa, but it is difficult to imagine the earliest hominids resisting such sweet temptation. Whenever honey gathering began, humans have apparently had a capable and energetic partner in their searches.

Figure 15.22 The greater honeyguide, *Indicator indicator*.

Guiding Behavior

The mutualistic association between humans and honeyguides may have developed from an earlier association between the bird and the ratel, or honey badger, *Mellivora capensis*. The honey badger is a powerful animal, well equipped with strong claws and powerful muscles to rip open bees' nests, but usually follows honeyguides to bees' nests. The honey badger, though secretive, has been observed often following honeyguides while vocalizing. African honey gatherers also vocalize to attract honeyguides, and Friedman (1955) reported that some of their vocalizations imitate the calls of honey badgers.

The most detailed and quantitative study of this mutualism to date is that of H. Isack of the National Museum of Kenya and H.-U. Reyer of the University of Zurich (Isack and Reyer 1989), who studied the details of the interaction of the greater honeyguide with the Boran people of northern Kenya. The Boran regularly follow honeyguides and have developed a pounding whistle that they use to attract them. The whistle can be heard over 1 km away, and Isack and Reyer found that it doubles the rate at which Boran honey gatherers encounter honeyguides. If they are successful in attracting a honeyguide, the average amount of time it takes to find a bees' nest is 3.2 hours. Without the aid of a honeyguide the

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Information
Hypothesis
Predictions
✓ Testing

Investigating the Evidence 13

Field Experiments

Field experiments have played a key role in the assessment of the importance of competitive interactions in nature. Joseph Connell (1974) and Nelson Hairston, Sr. (1989), two of the pioneers in the use of field experiments in ecology, outlined their proper design and execution. Connell points out that one of the most substantial differences between laboratory and field experiments is that in the laboratory setting, the investigator controls all important factors but one, the factor of interest. In contrast, in field experiments, all factors are allowed to vary naturally (the investigator generally has no choice) while the factor of interest is controlled, or manipulated, by the investigator.

Both laboratory and field experiments have played an important role in ecology, but it is the field experiment that provides the key to unlock the secrets of complex interactions in nature. Why is it that field experiments are more useful in this regard? Connell pointed out that compared to laboratory experiments, the results of field experiments can be more directly applied to understanding relationships in nature because "interactions with other organisms, and the natural variation in the abiotic environment, are included in the experiment." The best field experiments are those that are executed with the least disturbance to the natural community. The utility of field experiments, however, depends upon several design features.

Knowledge of Initial Conditions

To test for change in response to experimental manipulation, you have to know what conditions were like before the manipulation. Departures from initial conditions indicate a response to the experimental treatments. For instance, in his experiments on competition between barnacles, Connell first estimated the initial population density of one of the species in all his study plots (see fig. 13.19). Brown and his colleagues (Brown and Munger 1985, Heske, Brown, and Mittelbach 1994) were also careful to measure the population densities of all rodent species in their study plots several times before excluding large granivorous rodents from their experimental plots.

Controls

As in laboratory experiments, field experiments must include controls. Without controls it would be impossible to determine whether or not an experimental treatment has had an effect. Tinsley (1917) created controls for his experiments on competition by growing each of his potential competitors by themselves in acidic and basic soils. What was the control for the experiment on competition among desert rodents? Brown's research team created controls by surrounding study plots with their mouse-proof fence but then cutting holes 6.5 cm in diameter in the fences to allow large granivorous rodents to move freely into and out of the plots.

Replication

Field experiments, where possible, should include replication. Why? Ecological systems and environmental conditions are variable, both in time and space. Replication is intended to capture this variation. The question posed by the experimenter is whether an experimental effect is apparent despite variation. Ecologists use statistics to make such a judgment. Without replication, you would never know if the results could be repeated either in time or space.

What is considered acceptable study design has changed over the decades, reflecting increasing familiarity and concern for statistical analysis. In Tinsley's experiments on how competition may restrict the distribution of *Gelium* species to particular soils, replication was totally lacking. In Tinsley's experiment each condition (soil type) was represented just one time. Connell's later experiments with barnacles included some replication, but it was still limited at each tidal level. However, since there was a great deal of consistency in response across tidal levels, we can accept that competition acts as a significant force limiting barnacle distributions within the intertidal zone. In contrast to these earlier experiments, the more recent experiments by Brown on competition among desert rodents were replicated sufficiently for statistical analysis and repeated a second time.

The reviews by Connell and Hairston provide a guide to field experimentation as it has been conducted in the past few decades. However, as we shall see in section VI, the need for experimentation at large scales in finding ecologists to further expand their concept of experimental design.

Criticizing the Evidence 13

1. Why did Brown's research team (see p. 300) create controls by completely fencing study plots and then cutting holes in their sides to allow free passage of rodents into and out of the plot? Why not just compare the density of small rodents in the large granivore removal plots with their densities in the surrounding desert?

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 reemphasize 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.

Note: Updated Suggested Readings are now located on the book's website at www.mhhe.com/molles5e.

End-of-Book Material:

- ***Appendixes*** One appendix, "Statistical Tables," is available to the student for reference. Answers to Concept Review questions and answers to Critiquing the Evidence are now available on the book's website at www.mhhe.com/molles5e.
- ***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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- Answers to review questions
- Answers to Critiquing the Evidence
- Class activities
- PowerPoint lecture presentations
- Interactive world maps

Computerized Test Bank

Also on the book's website, this feature contains a wealth of cross-platform (Windows and Macintosh) resources for the instructor. Supplements featured include a computerized test bank, which utilizes EZ Test software to quickly create customized exams. This flexible and user-friendly program allows instructors to search for questions by topic, format, or difficulty level, and edit existing questions or add new ones. Multiple versions of the test can be created, and any test can be exported for use with course management systems such as WebCT, Blackboard, or PageOut. Word files of the test bank are included for those instructors who prefer to work outside of the test-generator software. Other assets are grouped within easy-to-use folders.

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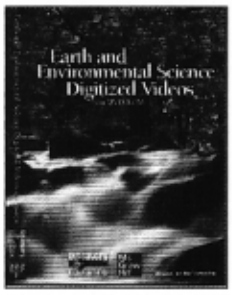

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- Practice quizzing
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- Animations
- Guide to electronic research
- Regional perspectives (case studies)
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- Periodic table
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***Ecology Laboratory Manual*, by Vodopich**
(ISBN: 978-0-07-338318-7;
MHID: 0-07-338318-X)

Darrell Vodopich, co-author of *Biology Laboratory Manual*, has written a new lab manual for ecology. This lab manual offers straightforward procedures that are doable in a broad range of classroom, lab and field situations. The procedures have specific instructions that can be taught by a teaching assistant with minimal experience as well as by a professor.

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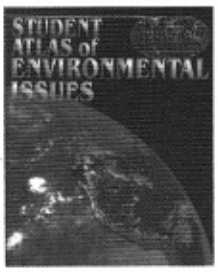

***Student Atlas of Environmental Issues*, by Allen**
(ISBN: 978-0-69-736520-0;
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This atlas is an invaluable pedagogical tool for exploring the human impact on the air, waters, biosphere, and land in every major world region. This informative resource provides a unique combination of maps and data that help students understand the dimensions of the world's environmental problems and the geographic 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 fifth 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, Robin Reed, Deb Henricks, Joan Weber, Tami Petsche, Dan Wallace, Brenda Rolwes, Melissa Leick, Judi David, Kay Brimeyer, 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 fifth 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.

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Lana Hamilton *Northeast State Tech Community College*
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