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

The introduction introduces two developing frontiers featured in several later chapters. One of those frontiers, urban ecology, has become a critical concern as the majority of humans now live in cities, a global proportion that is projected to approach 80 percent by mid-century. In an increasingly urbanized world, it is essential that we understand the ecology of cities. The second frontier, aeroecology, has emerged as new tools have become available to ecologists as they seek to understand the aerosphere, the relatively thin substratum of the atmosphere closest to the earth's surface that supports life. This developing frontier complements ecology's historical research emphasis on the geosphere and hydrosphere.

The conceptual foundations of chapters have been given more visibility and strengthened. The outline that opens each chapter now features the chapter's central concepts, bringing them to the immediate attention to the reader. In a number of chapters, the former concepts have been unpacked to improve the subject's conceptual outline.

A new contributor to the sixth edition introduces the field of ecological stoichiometry. Ecological stoichiometry is introduced and linked to energy and nutrient relations in chapter 7 and then further developed in chapter 19, which is concerned with nutrient cycling in ecosystems. The inclusion

of ecological stoichiometry acknowledges the vitality and growing appreciation of the importance of this area of ecology.

The present edition recognizes the call for developing student learning outcomes. Educators are being asked increasingly to develop concrete student learning outcomes for courses across the curriculum. Online support materials for the sixth edition include detailed student learning outcomes for all chapters. We propose that the general learning outcomes for the material covered in this text should include: (1) Define key terms; (2) Explain the main concepts disussed; (3) Evaluate the strength of research presented in support of the main concepts, including a critique of study design; (4) Interpret statistical evidence bearing on concepts, expressed in graphical and numerical form; (5) Apply the main concepts discussed to the interpretation of new situations.

New supplementary materials placed online. Suggested readings, answers to concept review questions and answers to critiquing the evidence questions are now online. As mentioned above, the online supplementary materials include student learning outcomes for all sections of all chapters. In addition, examples cut from the fifth and fourth editions are also available online.

New chapter opener photos and captions. The new photos that open all chapters are accompanied by a caption that links to the core content of each chapter. These photos and captions are intended to provide the reader with a window to the material to follow.

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 1,** the pedagogy included in later chapters has been added to reinforce the important concepts included in the introduction to ecology. Added material includes chapter concepts, concept review questions, a chapter summary, and chapter review questions. The ecological frontiers of urban ecology and aeroecology are also introduced.

In **chapter 3,** including a presentation of the river ecosystem synthesis model has expanded the breadth of the discussion of river ecology. In addition, the art representing the river continuum concept has been revised.

In **chapter 4,** two new case studies featuring stabilizing and disruptive selection have been added to complement an existing case study on directional selection. In addition, heritability information has been integrated with the evolutionary case studies.

In **chapter 5,** new photos contribute to the aeroecology thread in this edition. A photo showing the thermal radiator of a Brazilian free-tailed bat in the section on temperature regulation by endotherms is paired with a thermal image of the species in flight. Also, the principle of allocation has been separated under a new concept as a lead up to temperature and performance. The applications feature is tied more explicitly to this edition's urban ecology thread.

In **chapter 7,** the study of ecological stoichiometry is introduced within the context of energy and nutrient relations. This discussion is linked to additional material on ecological stoichiometry in chapter 19.

In **chapter 8,** an improved and expanded set of central concepts, combined with new concept review questions unpacks the chapter content. The material has also been edited to correct haplodiploidy's relationship to eusociality in light of recent information on mating in eusocial hymenoptera and discoveries of additional non-haplodiploid eusocial species.

In **chapter 10,** the roles of births, immigration, deaths, and emigration in population dynamics are reinforced and clarified with an equation and introductory paragraph. The presentation also connects contemporary shifts in species altitudinal and latitudinal ranges with climate warming. A new figure provides a graphic representation of a metapopulation (of butterflies).

In **chapter 11,** the use of r_{max}, intrinsic rate of increase, is clarified and corrected by limiting it to the logistic growth model; the model for exponential growth simply uses r, per capita rate of increase. A discussion of the significance of immigration and emigration to human populations connects back to the introduction to population dynamics in chapter 10. Human population statistics have been updated to 2011.

In **chapter 12,** Charnov's newer planar life history classification of birds, mammals, and lizards has been substituted for his earlier life history cube.

In **chapter 14,** the aeroecology thread is continued with two sections on bat foraging, including several new figures. In the first, evidence for bird versus bat limitation of foliage arthropods in tropical lowland forest is examined. The second section is a new applications feature focused on the economic value of pest control by bats.

In **chapter 16,** the new applications feature examines urban diversity, forming part of the urban ecology thread in this edition.

In **chapter 19,** there is a new discussion of the stoichiometry of aquatic vertebrates. The role of plants in nutrient

dynamics has been strengthened, including an improved presentation of the Hubbard Brook whole watershed experiment, which is tied to studies on the role of vegetation in limiting nutrient losses following the Yellowstone fires. A new application featuring the influence of cities on nutrient fluxes continues the urban ecology thread.

In **chapter 20,** including two new photos illustrating the extent of glacial retreat during historic times has strengthened the presentation of succession at Glacier Bay, Alaska.

In **chapter 23,** the Antarctic ozone hole discussion has been updated to 2010, including 32 years of data from NASA fitted with a highly significant curve, suggesting initial stages of ozone recovery.

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 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. Each concept discussion ends with a series of concept review questions to help students test their knowledge.

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


72 Section I Natural History and Evolution

(a) (b)

Figure 3.41 Two invaders of the Great Lakes: (a) sea lampreys, shown here attached to a lake trout; and (b) zebra mussels, encrusting a host mollusc. Invading species, such as these, have created ecological disasters in freshwater ecosystems around the globe.

Concept 3.2 Review

1. After years of successful reductions in phytoplankton populations, phytoplankton blooms are on the increase in parts of Lake Erie following the introduction of zebra mussels. Why?
2. Why is the prospect of global warming considered a serious threat to coral reefs?
3. Why do physiologically tolerant rather than sensitive species inhabit estuaries and salt marshes?

Applications

Biological Integrity—Assessing the Health of Aquatic Systems

How can we put our knowledge of the natural history of aquatic life to work? A major question that biologists often face is whether a particular influence impairs the health of an aquatic system. Natural history information can play a significant role in making that judgment. Given the complex array of potential human impacts on aquatic systems, what might we use as indicators of health? An answer to this question has been proposed by James Karr and his colleagues, who suggest that we consider what they call "biological integrity," which they define as "a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of the natural habitat of the region" (Karr and Dudley 1981). These researchers proposed that a healthy aquatic community is one that is similar to the community in an undisturbed habitat in the same region. The community should be "balanced" and "integrated." Deciding what constitutes this state requires judgment based on broad knowledge of the habitats in question and their inhabitants—that is, knowledge of natural history. If we could assess the health, as defined by Karr, of a community of aquatic organisms, we would have gone a long way toward assessing the health of the aquatic ecosystem of which this community is part.

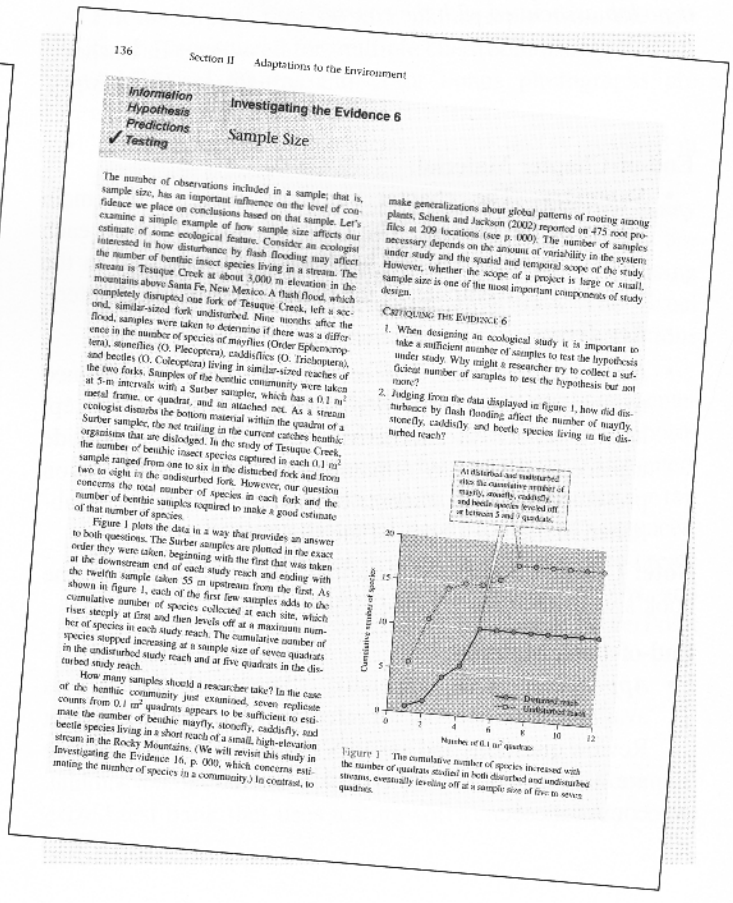
Moving beyond general definitions and broad goals, Karr developed an Index of Biological Integrity (IBI) and applied his index to fish communities. Fish communities were chosen because we know a lot about fish and their habitat requirements and they are relatively easy to sample. Karr's index has three categories for rating a stream or river:

1. number of species and species composition, which includes the number, kinds, and tolerances of fish species;
2. trophic composition, which considers the dietary habits of the fish making up the community;
3. fish abundance and condition.

Under these three categories there are 12 attributes of the fish community. The stream is assigned a score of 5, 3, or 1 for each attribute, where 5 equals best and 1 equals worst. The scores on all the attributes are added to give a total score that ranges from 12 (poor biological integrity) to 60 (excellent biological integrity). Notice that Karr has built a safeguard into his index. Judging several attributes of the fish community eliminates the bias that might creep in if assessments were made from only one or a very few attributes. In the following sections, we will examine the three community characteristics.

Number of Species and Species Composition

Heavy human impact generally reduces the number of native species in a community while increasing the number


136 Section II Adaptations to the Environment

Information Hypothesis Predictions ✓ Testing

Investigating the Evidence 6

Sample Size

The number of observations included in a sample; that is, sample size, has an important influence on the level of confidence we place on conclusions based on that sample. Let's examine a simple example of how sample size affects our estimate of some ecological feature. Consider an ecologist interested in how disturbance by flash flooding may affect the number of benthic insect species living in a stream. The stream is Tesuque Creek at about 3,000 m elevation in the mountains above Santa Fe, New Mexico. A flash flood, which completely disrupted one fork of Tesuque Creek, left a second, similar-sized fork undisturbed. Nine months after the flood, samples were taken to determine if there was a difference in the number of species of mayflies (Order Ephemeroptera), stoneflies (O. Plecoptera), caddisflies (O. Trichoptera), and beetles (O. Coleoptera) living in similar-sized reaches of the two forks. Samples of the benthic community were taken at 5-m intervals with a Surber sampler, which has a 0.1 m^2 metal frame, or quadrat, and an attached net. As a stream ecologist disturbs the bottom material within the quadrat of a Surber sampler, the net trailing in the current catches benthic organisms that are dislodged. In the study of Tesuque Creek, the number of benthic insect species captured in each 0.1 m^2 sample ranged from one to six in the disturbed fork and from two to eight in the undisturbed fork. However, our question concerns the total number of species in each fork and the number of benthic samples required to make a good estimate of that number of species.

Figure 1 plots the data in a way that provides an answer to both questions. The Surber samples are plotted in the exact order they were taken, beginning with the first that was taken at the downstream end of each study reach and ending with the twelfth sample taken 55 m upstream from the first. As shown in figure 1, each of the first few samples adds to the cumulative number of species collected at each site, which rises steeply at first and then levels off at a maximum number of species in each study reach. The cumulative number of species stopped increasing at a sample size of seven quadrats in the undisturbed study reach and at five quadrats in the disturbed study reach.

How many samples should a researcher take? In the case of the benthic community just examined, seven replicate counts from 0.1 m^2 quadrats appears to be sufficient to estimate the number of benthic mayfly, stonefly, caddisfly, and beetle species living in a short reach of a small, high-elevation stream in the Rocky Mountains. (We will revisit this study in Investigating the Evidence 16, p. 000, which concerns estimating the number of species in a community.) In contrast, to make generalizations about global patterns of rooting among plants, Schenk and Jackson (2002) reported on 475 root profiles at 209 locations (see p. 000). The number of samples necessary depends on the amount of variability in the system under study and the spatial and temporal scope of the study. However, whether the scope of a project is large or small, sample size is one of the most important components of study design.

CRITIQUING THE EVIDENCE 6

1. When designing an ecological study it is important to take a sufficient number of samples to test the hypothesis under study. Why might a researcher try to collect a sufficient number of samples to test the hypothesis but not more?
2. Judging from the data displayed in figure 1, how did disturbance by flash flooding affect the number of mayfly, stonefly, caddisfly, and beetle species living in the disturbed reach?

Figure 1 The cumulative number of species increased with the number of quadrats studied in both disturbed and undisturbed streams, eventually leveling off at a sample size of five to seven quadrats.

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. Each Evidence box ends with one or more questions, under the heading "Critiquing the Evidence," which are designed to stimulate critical thinking about the box content.

"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

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/molles6e.

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/molles6e.
- ***Glossary*** List of all key terms and their definitions.
- ***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

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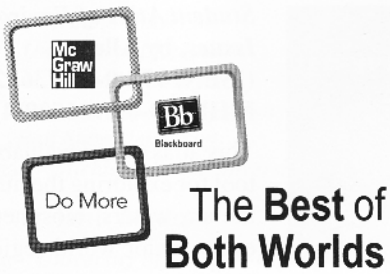

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This text-specific website offers an extensive array of teaching tools. In addition to all of the student assets available, this site includes:

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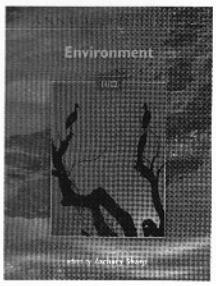
- **PowerPoint® Lecture Outlines** Ready-made presentations written by Peter Stiling that combine art and photos and lecture notes are provided for each of the 23 chapters of the text. These outlines can be used as they are, or tailored to reflect your preferred lecture topics and sequences.
- **PowerPoint® 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.

Test Bank

The test bank contains a variety of questions. This computerized test bank that uses testing software to quickly create

customized exams is available on the text website. The user-friendly program allows instructors to search for questions by topic or format, edit existing questions or add new ones; and scramble questions for multiple versions of the same test. Word files of the test bank questions are provided for those instructors who prefer to work outside the test-generator software.



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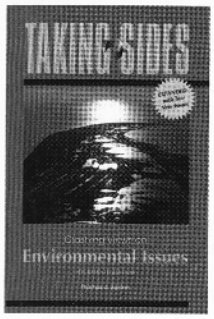

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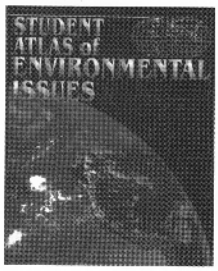
***Ecology Laboratory Manual,* by Vodopich**
(ISBN: 978-0-07-338318-7;
MHID: 0-07-338318-X)

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.



***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 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 sixth 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: Art Benke, Eric Charnov, Scott Collins, Cliff Dahm, Thomas Kunz, Tim Lowrey, Will Pockman, Jon Reichard, Jim Thorpe, Eric Toolson, Lawrence Walker, and Chris Witt. 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 Becky Olson, Lori Bradshaw, Joan Weber, Dan Wallace, Tara McDermott, Kelly Heinrichs, Judi David, 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 sixth edition. Their depth and breadth of knowledge and experience, both as researchers and teachers, are humbling. They continue my education, for which I am grateful, and I honestly could not have continued the improvement of this textbook without them.

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