Manuel C. Molles Jr. is an emeritus Professor of Biology at the University of New Mexico, where he has been a member of the faculty and curator in the Museum of Southwestern Biology since 1975 and where he continues to teach ecology and advise graduate students. He received his B.S. from Humboldt State University and his Ph.D. from the Department of Ecology and Evolutionary Biology at the University of Arizona. Seeking to broaden his geographical perspective, he has taught and conducted ecological research in Latin America, the Caribbean, and Europe. He was awarded a Fulbright Research Fellowship to conduct research on river ecology in Portugal and has held visiting professor appointments in the Department of Zoology at the University of Coimbra, Portugal, in the Laboratory of Hydrology at the Polytechnic University of Madrid, Spain, and at the University of Montana’s Flathead Lake Biological Station.

Originally trained as a marine ecologist and fisheries biologist, the author has worked mainly on river and riparian ecology at the University of New Mexico. His research has covered a wide range of ecological levels, including behavioral ecology, population biology, community ecology, ecosystem ecology, biogeography of stream insects, and the influence of a large-scale climate system (El Niño) on the dynamics of southwestern river and riparian ecosystems. His current research concerns the influence of climate change and climatic variability on the dynamics of populations and communities along steep gradients of temperature and moisture in the mountains of the Southwest. Throughout his career, Dr. Molles has attempted to combine research, teaching, and service, involving undergraduate as well as graduate students in his ongoing projects. At the University of New Mexico, he has taught a broad range of lower division, upper division, and graduate courses, including Principles of Biology. Evolution and Ecology, Stream Ecology, Limnology and Oceanography, Marine Biology, and Community and Ecosystem Ecology. He has taught courses in Global Change and River Ecology at the University of Coimbra, Portugal, and General Ecology, and Groundwater and Riparian Ecology at the Flathead Lake Biological Station. Dr. Manuel Molles was named Teacher of the Year by the University of New Mexico for 1995–96 and Potter Chair in Plant Ecology in 2000.
Dedication

To Mary Anne and Misha
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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
In chapter 6, I added material on the evolution, diversity, and significance of C₄ plants, and cross-referenced materials to chapters 18 (Liebig’s law), 19 (nutrient cycling), and 23 (atmospheric CO₂ 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. LTTER Network and the International LTTER network, including an update of the map of the U.S. LTTER 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.

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.

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 appendices 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.
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

“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. Buscher
Boston University

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

**Application**

Using Proportion to Control a Parameter

Pounding disease affects approximately 30% of married women in some areas of the world, producing a variety of health problems including infertility, stillbirth, and neonatal death. Because research is curtailed in such areas, cautious optimism is the best approach in developing effective strategies to control the problem. This is a complex parameter that is difficult to measure, but proportional data can be used to develop effective strategies. We assume that a parameter is directly proportional to the number of years of age. That is, as the number of years of age increases, so does the parameter.

![Diagram of a normal distribution, showing the percentage of observations about the mean, and these standard deviations of the mean.](Figure 11.29)
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.

- **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 Supplements for Instructors

**Online Learning Center (OLC)**  
(www.mhhe.com/molles4e)

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

- Answers to review questions
- Class activities
- PowerPoint lecture presentations
- Interactive world maps
- eInstruction questions
- List of transparencies

**OLC Presentation Center (found at www.mhhe.com/molles4e)**

*Build instructional materials where-ever, when-ever, and how-ever you want!*

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Instructors will find the following digital assets for *Ecology: Concepts and Applications* at OLC Presentation Center:

- **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.

### 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.
• **Videos** This special collection of 71 underwater video clips displays interesting habitats and behaviors for many animals in the ocean.

• **Animations** 100 full-color animations that illustrate many different concepts covered in the study of ecology are available for use in creating classroom lectures, testing materials, or online course communication. The visual impact of motion will enhance classroom presentations and increase comprehension.

• **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.

Earth and Environmental Science DVD by Discovery Channel Education (ISBN: 978-0-07-352541-9; MHID: 0-07-352541-3)

Begin your class with a quick peek at science in action. The exciting NEW DVD by Discovery Channel Education offers 50 short (3–5 minute) videos on topics ranging from conservation to volcanoes. Search by topic and download into your PowerPoint lecture.


Licensed from some of the highest quality life science video producers in the world, these brief video clips on DVD range in length from 15 seconds to two minutes and cover all areas of general biology, from cells to ecosystems. Engaging and informative, McGraw-Hill’s digitized biology videos will help capture students’ interest while illustrating key biological concepts, applications, and processes.

Instructor’s Testing Resource CD-ROM

This CD-ROM contains a wealth of cross-platform (Windows and Macintosh) resources for the instructor. Supplements featured on this CD-ROM 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 on the Instructor’s Testing and Resource CD-ROM are grouped within easy-to-use folders.


A set of 100 overhead transparencies includes key illustrations and tables from the text. The images are printed for great visibility and contrast, and labels are large and bold for clear projection.

**eInstruction**

This classroom performance system (CPS) utilizes wireless technology to bring interactivity into the classroom or lecture hall. Instructors and students receive immediate feedback through wireless response pads that are easy to use and engage students. eInstruction can assist instructors by:

• Taking attendance
• Administering quizzes and tests
• Creating a lecture with intermittent questions
• Using the CPS grade book to manage lectures and student comprehension
• Integrating interactivity into PowerPoint presentations

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**Course Delivery Systems**

With help from WebCT, Blackboard, and other course management systems, professors can take complete control of their course content. Course cartridges containing website content, online testing, and powerful student tracking features are readily available for use within these platforms.

**Learning Supplements for Students**

**Online Learning Center (OLC)** (www.mhhe.com/molles4e)

This text-specific website offers a wide variety of student resources providing many opportunities to master the core concepts in ecology. Learn more about the exciting features provided for students through the **Ecology: Concepts and Applications** website:

• 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
Preface


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.


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.


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.


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.


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.


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.


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
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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

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Manuel C. Molles Jr.