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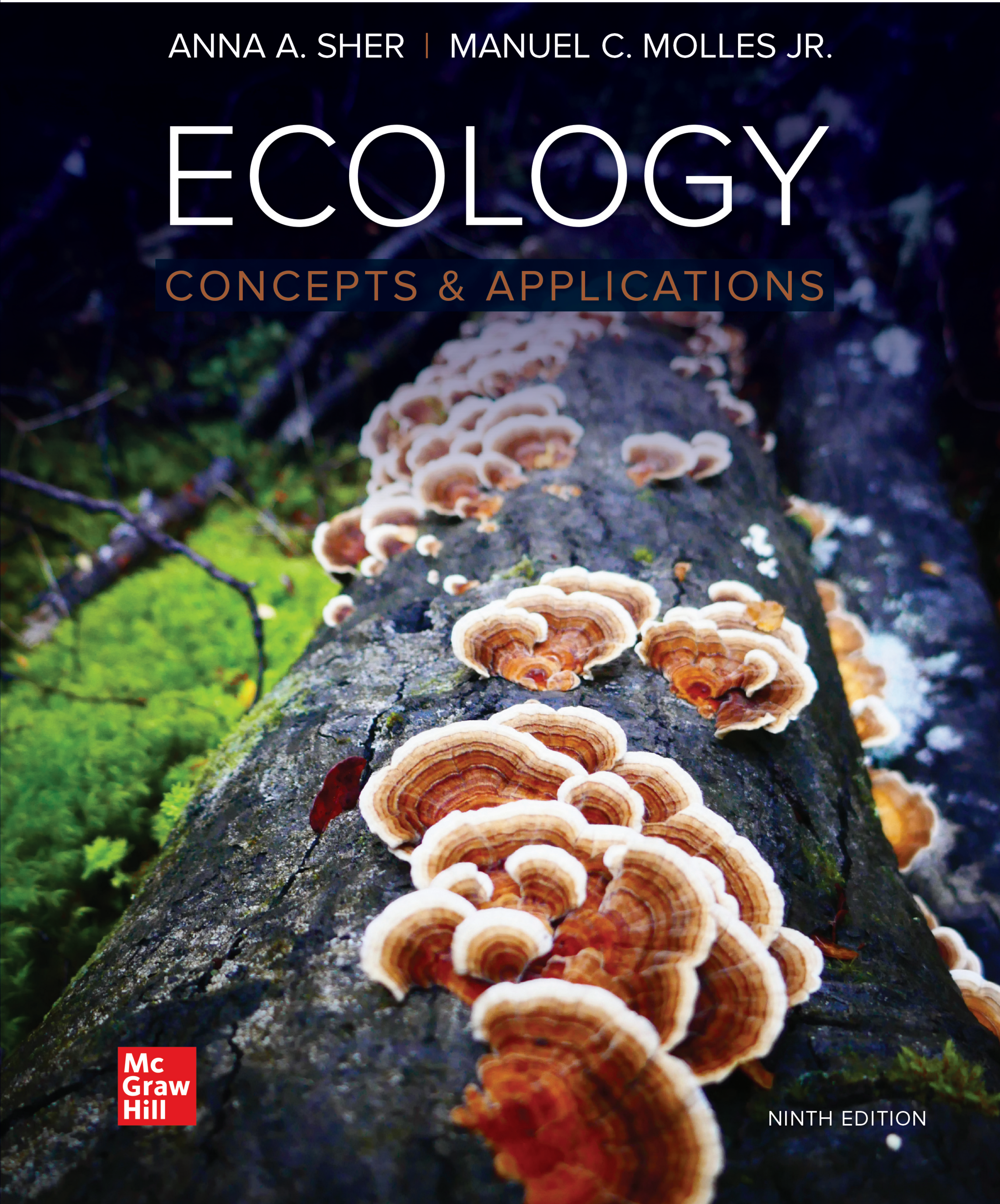
ANNA A. SHER | MANUEL C. MOLLES JR.

ECOLOGY

CONCEPTS & APPLICATIONS



NINTH EDITION

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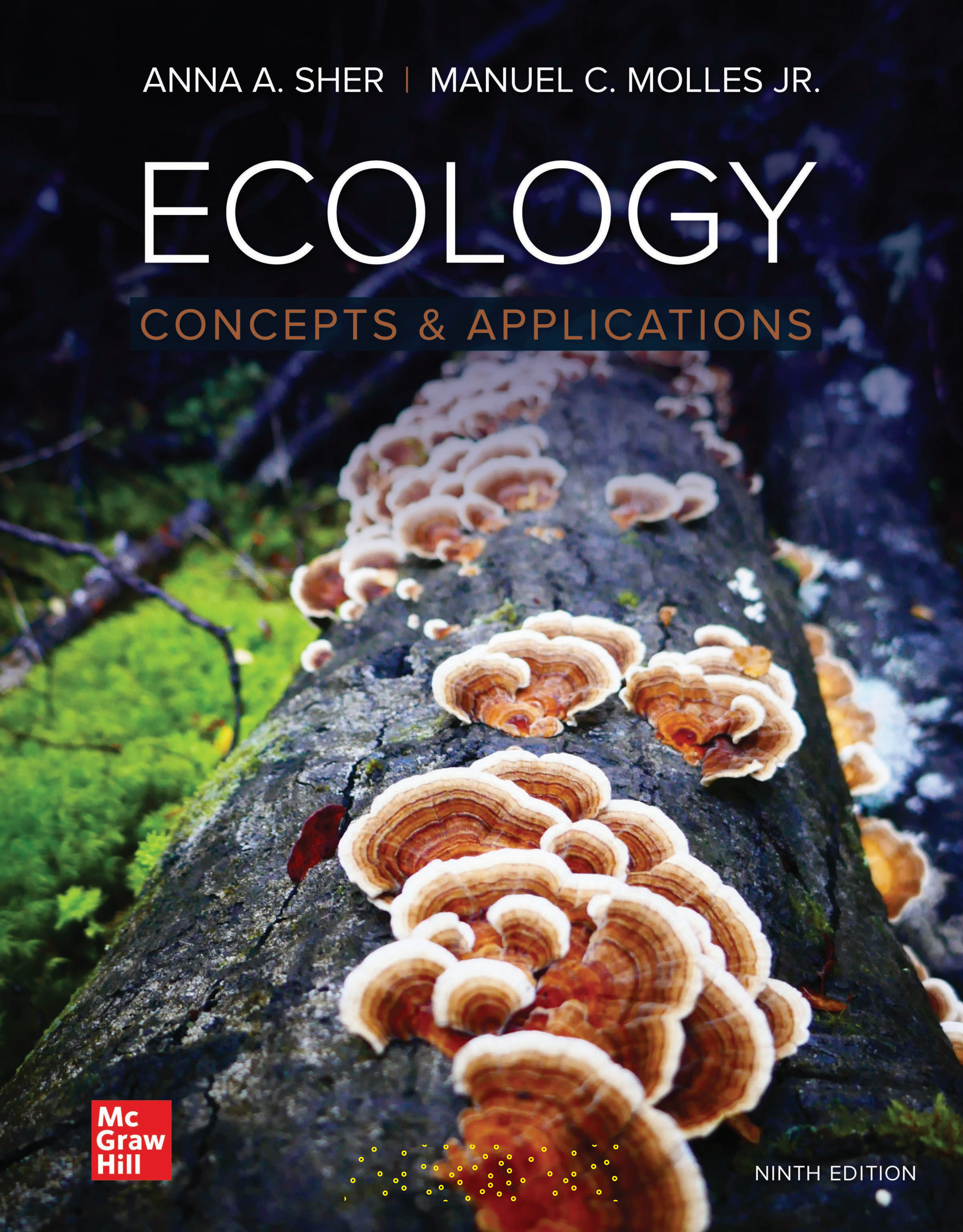

McGraw Hill

NINTH EDITION

ECOLOGY

Published by McGraw Hill LLC, 1325 Avenue of the Americas, New York, NY 10019.

This book is printed on acid-free paper.

1 2 3 4 5 6 7 8 9 LWI 26 25 24 23 22 21

ISBN 978-1-265-28633-0
MHID 1-265-28633-7

Cover Image: *Anna A. Sher*

mheducation.com/highered

About the Authors

Courtesy of Anna Sher

Anna A. Sher is a full professor in the Department of Biological Sciences at the University of Denver, where she has been faculty since 2003. Until 2010 she held this position jointly with the Denver Botanic Gardens as the Director of Research and Conservation. As a student, she was a double major in Biology and Art at Earlham College, where she has also taught ecology, and was the co-leader of the Earlham Study Abroad Kenya Program. She received her PhD from the University of New Mexico, where she also taught botany as a visiting lecturer. As a postdoctoral researcher, Dr. Sher was awarded a Fulbright postdoctoral research fellowship to conduct research on plant interactions in Israel at Ben Gurion University's Mitrani Department of Desert Ecology, and she also studied the ecology of an invasive grass at the University of California, Davis. She has also been a visiting professor at the University of Otago, Dunedin, New Zealand.

Dr. Sher's primary research focus has been on the ecological dynamics associated with the removal of invasive riparian plants. She is known as a leading expert in the ecology of *Tamarix,* a dominant exotic tree, and she was the lead editor of the first book exclusively on the topic. Her research interests and publications have spanned several areas within ecology, including not only restoration ecology, competition, and invasive species ecology, but also interactions between plants and soil chemistry, mycorrhizae, insect diversity and trophic cascades, ethnobotany, phenology, climate change, and rare species conservation. She is also lead author of the textbook series *An Introduction to Conservation Biology* (Oxford University Press). Dr. Sher has a particular interest in quantitative ecological methods, with her lab specializing in multivariate methods and spatial models at both individual organism and regional scales. She is currently principal investigator of a National Science Foundation award to investigate the human dimension of the restoration of damaged ecosystems, and she has been a TEDx speaker on the way ecosystems can teach us how to solve human problems.

Above all, Dr. Sher loves to teach and mentor students doing research at both undergraduate and graduate levels.

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. He received his BS from Humboldt State University and his PhD from the Department of Ecology and Evolutionary Biology at the University of Arizona. Seeking to broaden his geographic 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 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 interests focus on 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 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 1995–1996 and Potter Chair in Plant Ecology in 2000. In 2014, he received the Eugene P. Odum Award from the Ecological Society of America based on his "ability to relate basic ecological principles to human affairs through teaching, outreach and mentoring activities."

Courtesy of Manuel Molles

Design elements: Anna A. Sher

Dedication

To the Sher Lab and the whole next generation
of ecologists, who inspire me to do this work.
Also, I dedicate this edition to my co-author
and mentor, Manuel.
–Anna A. Sher

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501-1333

Design elements: Anna A. Sher

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LARGE-SCALE ECOLOGY

Appendix A Investigating the Evidence

Design elements: Anna A. Sher

Preface

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

Organization of the Book

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 earth's biomes—life on land and life in water—followed by 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, including chapters on landscape, geographic, and global ecology. These topics were first introduced in section I within its discussion of the biomes. In summary, the book begins with an overview of the biosphere, considers portions of the whole in the middle chapters, and ends with another perspective of the entire planet in the concluding chapter. The features of this textbook were carefully planned to enhance the students' comprehension of the broad discipline of ecology.

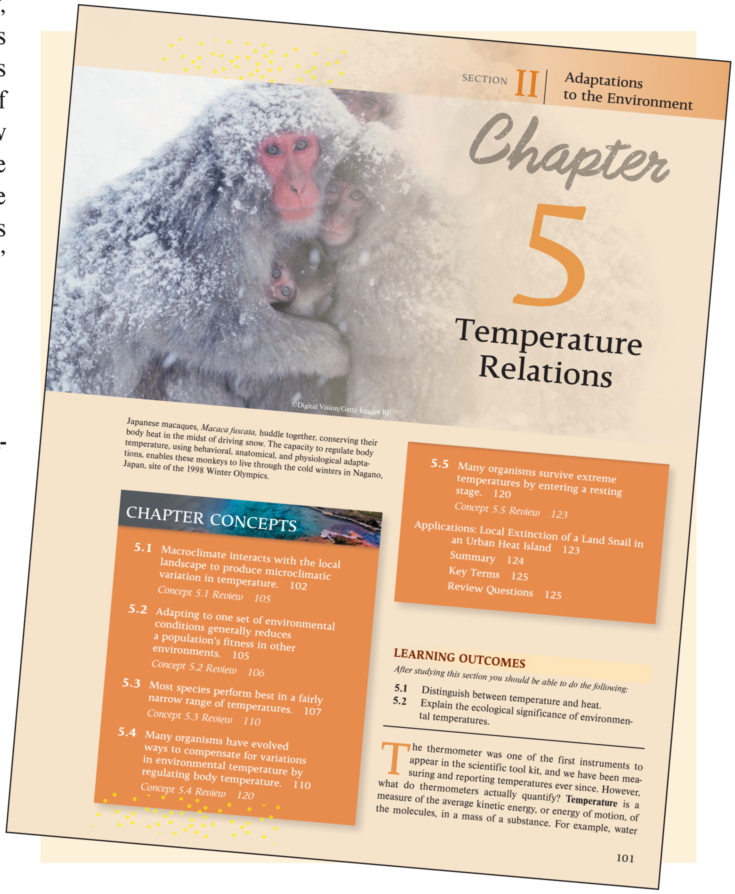
Features Designed with the Student in Mind

All chapters are based on a distinctive learning system, featuring the following key components:

Student Learning Outcomes: Educators are being asked increasingly to develop concrete student learning outcomes for courses across the curriculum. In response to this need and to help focus student progress through the content, all sections of each chapter in the ninth edition begin with a list of detailed student learning outcomes.

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, which are listed at the beginning of each chapter 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 covered in each chapter. The sections in which concepts are discussed focus on published studies and, wherever possible, the scientists who did the research are introduced. 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 and to reinforce key points made in the discussion.



SECTION II | Adaptations to the Environment

Chapter 5

Temperature Relations

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Japanese macaques, *Macaca fuscata,* huddle together, conserving their body heat in the midst of driving snow. The capacity to regulate body temperature, using behavioral, anatomical, and physiological adaptations, enables these monkeys to live through the cold winters in Nagano, Japan, site of the 1998 Winter Olympics.

CHAPTER CONCEPTS

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5.2 Adapting to one set of environmental conditions generally reduces a population's fitness in other environments. 105
Concept 5.2 Review 106

5.3 Most species perform best in a fairly narrow range of temperatures. 107
Concept 5.3 Review 110

5.4 Many organisms have evolved ways to compensate for variations in environmental temperature by regulating body temperature. 110
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LEARNING OUTCOMES

After studying this section you should be able to do the following:

5.1 Distinguish between temperature and heat.
5.2 Explain the ecological significance of environmental temperatures.

The thermometer was one of the first instruments to appear in the scientific tool kit, and we have been measuring and reporting temperatures ever since. However, what do thermometers actually quantify? **Temperature** is a measure of the average kinetic energy, or energy of motion, of the molecules, in a mass of a substance. For example, water

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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. The approach also provides an ongoing tutorial on graph interpretation, a skill with which many introductory students need practice.

Detailed Explanations of Mathematics: The mathematical aspects of ecology commonly challenge many students taking their first ecology course. This text carefully explains all mathematical expressions that arise to help students overcome these challenges. In some cases, mathematical expressions are dissected in illustrations designed to complement their presentation in the associated narrative.

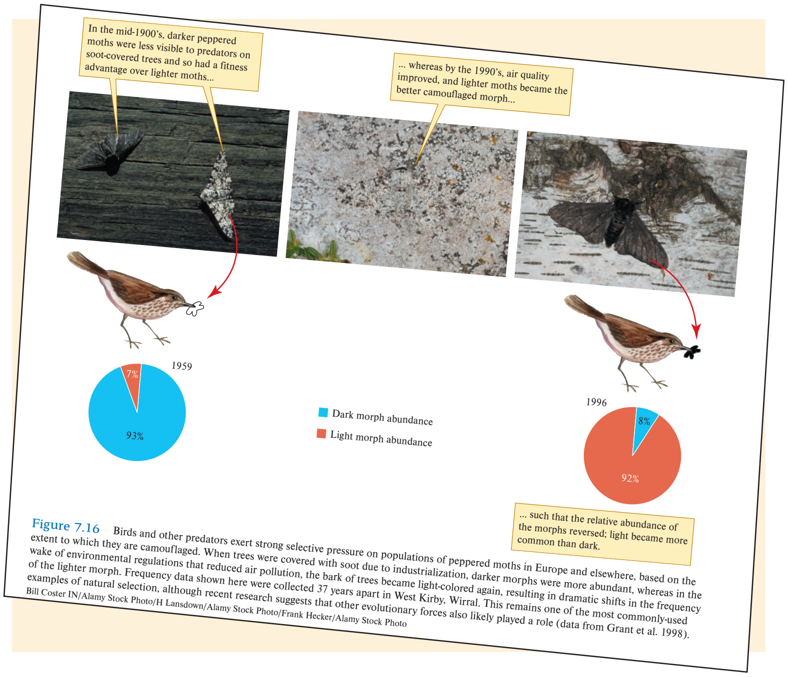
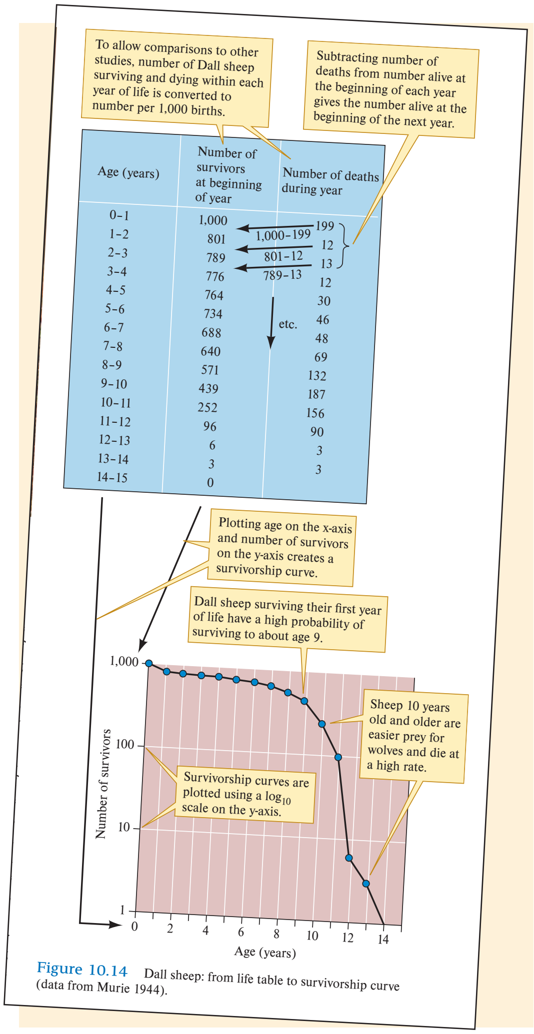


Figure 7.16 Birds and other predators exert strong selective pressure on populations of peppered moths in Europe and elsewhere, based on the extent to which they are camouflaged. When trees were covered with soot due to industrialization, darker morphs were more abundant, whereas in the wake of environmental regulations that reduced air pollution, the bark of trees became light-colored again, resulting in dramatic shifts in the frequency of the lighter morph. Frequency data shown here were collected 37 years apart in West Kirby, Wirral. This remains one of the most commonly-used examples of natural selection, although recent research suggests that other evolutionary forces also likely played a role (data from Grant et al. 1998).

Bill Coster IN/Alamy Stock Photo/H Lansdown/Alamy Stock Photo/Frank Hecker/Alamy Stock Photo

A visualization of a population bottle neck, using data from published research.



Age (years)	Number of survivors at beginning of year	Number of deaths during year
0–1	1,000	199
1–2	801	12
2–3	789	13
3–4	776	12
4–5	764	30
5–6	734	46
6–7	688	48
7–8	640	69
8–9	571	132
9–10	439	187
10–11	252	156
11–12	96	90
12–13	6	3
13–14	3	3
14–15	0	

Figure 10.14 Dall sheep: from life table to survivorship curve (data from Murie 1944).

Helps students work with and interpret quantitative information, involving converting numerical information into a graph.

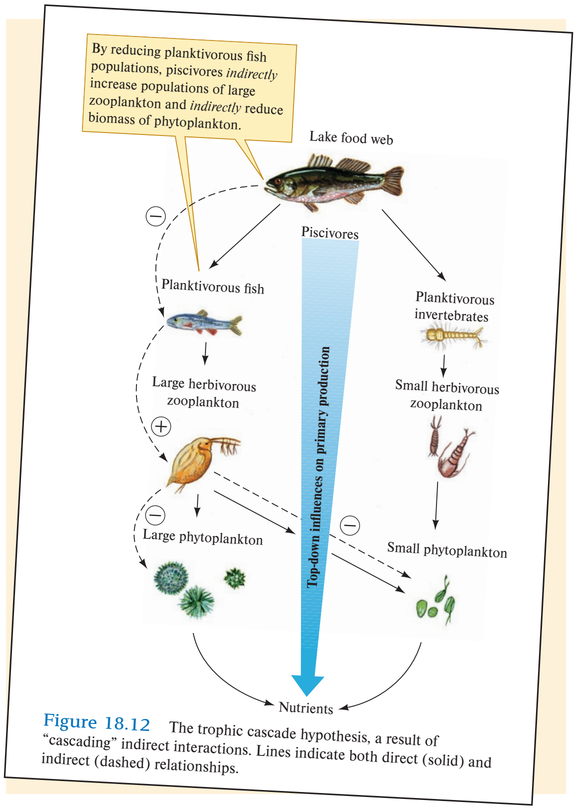


Figure 18.12 The trophic cascade hypothesis, a result of "cascading" indirect interactions. Lines indicate both direct (solid) and indirect (dashed) relationships.

Provides a visual representation of a hypothesis involving a set of complex ecological interactions.

Applications: Many students are concerned with the practical side of ecology and want to know more about how the tools of science can be applied to the environmental problems we face in the contemporary world. Including a discussion of applications at the end of each chapter can motivate 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.

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: Suggested Readings are located online.

End-of-Book Material:

- ***Appendixes*** Appendix A, "Investigating the Evidence," offers "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 explanations. The series of features begins with an overview of the scientific method, which establishes a conceptual context for more specific material in the next 21 features. The last reading wraps up the series with a discussion of electronic literature searches. Each Investigating the Evidence ends with one or more questions, under the heading "Critiquing the Evidence." This feature is intended to stimulate critical thinking about the content. Appendix B, "Statistical Tables," is available to the student as a reference in support of the Investigating the Evidence features. Appendix C, "Abbreviations" is a handy guide to the scientific and other abbreviations used throughout the text, including units of measurement. Appendix D is a global map of the biomes.
- ***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.
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Estimating the Number of Species in Communities

LEARNING OUTCOMES

After studying this section you should be able to do the following:

16.1 Explain the difficulties involved in trying to estimate the total number of species in a community.
16.2 Discuss ways to reduce the effort necessary for making a comparison of the relative species richness of communities.

How many species are there? This is one of the most fundamental questions that an ecologist can ask about a community. With increasing threats to biological diversity, species richness is also one of the most important community attributes we might measure. For instance, estimates of species richness are critical for determining areas suitable for conservation, for diagnosing the impact of environmental change on a community, and for identifying critical habitat for rare or threatened species. However, determining the number of species in a community is not a simple undertaking. Sound estimates of species richness for most taxa require a carefully designed, standardized sampling program. Here we will review some of the basic factors that an ecologist needs to consider when designing such a sampling program to gather information about species richness within and among communities.

Sampling Effort

The number of species recorded in a sample of a community increases with higher sampling effort. We reviewed a highly simplified example of this in Investigating the Evidence 6, where we considered how numbers of quadrats influenced estimates of species richness in the benthic community of a small Rocky Mountain stream. In that example, a relatively small sample size was required. However, often far more effort is required. For example, Petri Martikainen and Jari Kouki (2003) estimated that to verify the presence or absence of threatened beetle species in the boreal forests of Finland required a sample of over 400 beetle species. They also suggested that a sample of over 100,000 individual beetles may be required to assess just 10 forest areas in Finland for their suitability to serve as conservation areas for threatened beetle species. To reduce the sampling effort required to estimate species richness, community ecologists and conservationists often focus on groups of organisms that are reliable indicators of species richness.

Indicator Taxa

Because of the great cost and time of making thorough inventories of species diversity, ecologists have proposed a wide variety of taxa as indicators of overall biological diversity. Indicator taxa have generally been well-known and conspicuous groups of organisms such as birds and butterflies. However, it appears that indicator taxa need to be chosen with caution. For example, John Lawton of Imperial College in the United Kingdom and 12 colleagues (Lawton et al. 1998) attempted to characterize biological diversity along a disturbance gradient in the tropical forest of Cameroon, Africa, using indicator taxa. In addition to birds and butterflies, Lawton and his colleagues sampled flying beetles, beetles living in the forest canopy, canopy ants, leaf-litter ants, termites, and soil nematodes. They sampled these taxa from 1992 to 1994 and spent several more years sorting and cataloging the approximately 2,000 species collected. This work required approximately 10,000 scientist hours. Unfortunately, the conclusion at the end of this massive study was that no one group serves as a reliable indicator of species richness for other taxonomic groups. Lawton and his colleagues estimated that their survey included from one-tenth to one-hundredth the total number of species in their study site. Citing their own experience, they concluded that characterizing the full biological diversity of just 1 hectare of tropical forest would require from 100,000 to 1 million scientist hours. As a consequence of these time constraints, ecologists will likely continue to focus their studies of diversity on smaller groups of taxa. However, even with a restricted taxonomic focus, it is important to standardize sampling across study communities.

Standardized Sampling

Standardizing sampling effort and technique is generally necessary to provide a valid basis for comparing species richness across communities. For example, Frode Ødegaard of the Norwegian Institute for Nature Research took great care to standardize sampling as he compared species richness among plant-feeding beetles living in a tropical dry forest and in a tropical rain forest in Panama (Ødegaard 2006). Ødegaard sampled both forests from a canopy crane that provided access to similar areas of forest (~0.8 ha). He standardized the amount of time he spent sampling each tree or vine, and he used the same sampling techniques in both forests. Ødegaard also sampled the beetles on approximately the same number of plant species—50 species in the dry forest and 52 in the rain forest. His efforts resulted in the capture of very similar numbers of individual beetles in the two forests: 35,479 in dry forest versus 30,352 in rain forest. However, his collections in rain forest included 37% more beetle species than in dry forest: 1,603 species in rain forest versus 1,165 in dry forest. Because Ødegaard took care to standardize sampling, we can conclude that the species richness of plant-feeding beetles was probably higher at his rain forest study site. If his sampling efforts were uneven, we could not reach such a conclusion.

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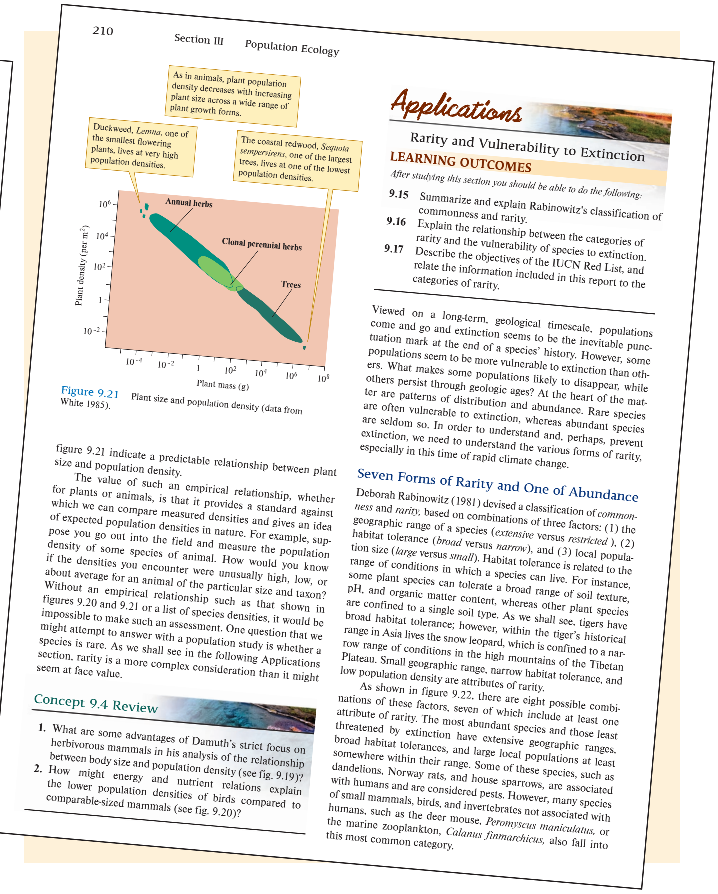
1. A complete list of species has not been determined for any area of substantial habitat anywhere on earth. Why not?
2. Why do most surveys of species diversity focus on restricted groups of relatively well-known organisms such as plants, mammals, and butterflies?



210 Section III Population Ecology

As in animals, plant population density decreases with increasing plant size across a wide range of plant growth forms.

Duckweed, *Lemna*, one of the smallest flowering plants, lives at very high population densities.

The coastal redwood, *Sequoia sempervirens*, one of the largest trees, lives at one of the lowest population densities.

Figure 9.21 Plant size and population density (data from White 1985).

figure 9.21 indicate a predictable relationship between plant size and population density.

The value of such an empirical relationship, whether for plants or animals, is that it provides a standard against which we can compare measured densities and gives an idea of expected population densities in nature. For example, suppose you go out into the field and measure the population density of some species of animal. How would you know if the densities you encounter were unusually high, low, or about average for an animal of the particular size and taxon? Without an empirical relationship such as that shown in figures 9.20 and 9.21 or a list of species densities, it would be impossible to make such an assessment. One question that we might attempt to answer with a population study is whether a species is rare. As we shall see in the following Applications section, rarity is a more complex consideration than it might seem at face value.

Concept 9.4 Review

1. What are some advantages of Damuth's strict focus on herbivorous mammals in his analysis of the relationship between body size and population density (see fig. 9.19)?
2. How might energy and nutrient relations explain the lower population densities of birds compared to comparable-sized mammals (see fig. 9.20)?

Applications

Rarity and Vulnerability to Extinction

LEARNING OUTCOMES

After studying this section you should be able to do the following:

9.15 Summarize and explain Rabinowitz's classification of commonness and rarity.
9.16 Explain the relationship between the categories of rarity and the vulnerability of species to extinction.
9.17 Describe the objectives of the IUCN Red List, and relate the information included in this report to the categories of rarity.

Viewed on a long-term, geological timescale, populations come and go and extinction seems to be the inevitable punctuation mark at the end of a species' history. However, some populations seem to be more vulnerable to extinction than others. What makes some populations likely to disappear, while others persist through geologic ages? At the heart of the matter are patterns of distribution and abundance. Rare species are often vulnerable to extinction, whereas abundant species are seldom so. In order to understand and, perhaps, prevent extinction, we need to understand the various forms of rarity, especially in this time of rapid climate change.

Seven Forms of Rarity and One of Abundance

Deborah Rabinowitz (1981) devised a classification of *commonness* and *rarity,* based on combinations of three factors: (1) the geographic range of a species (*extensive* versus *restricted*), (2) habitat tolerance (*broad* versus *narrow*), and (3) local population size (*large* versus *small*). Habitat tolerance is related to the range of conditions in which a species can live. For instance, some plant species can tolerate a broad range of soil texture, pH, and organic matter content, whereas other plant species are confined to a single soil type. As we shall see, tigers have broad habitat tolerance; however, within the tiger's historical range in Asia lives the snow leopard, which is confined to a narrow range of conditions in the high mountains of the Tibetan Plateau. Small geographic range, narrow habitat tolerance, and low population density are attributes of rarity.

As shown in figure 9.22, there are eight possible combinations of these factors, seven of which include at least one attribute of rarity. The most abundant species and those least threatened by extinction have extensive geographic ranges, broad habitat tolerances, and large local populations at least somewhere within their range. Some of these species, such as dandelions, Norway rats, and house sparrows, are associated with humans and are considered pests. However, many species of small mammals, birds, and invertebrates not associated with humans, such as the deer mouse, *Peromyscus maniculatus,* or the marine zooplankton, *Calanus finmarchicus,* also fall into this most common category.

New to the Ninth Edition

Nearly every chapter has significant changes in this edition. To update content and respond to reviewers' comments, we have incorporated the research and ideas of over 140 new citations, the majority of which (73%) were authored by underrepresented scientists. A particular effort was made to cite cutting-edge ecological research by women of color. With each edition, we continue toward the goal of making this text reflect the true diversity of researchers in the field.

There are over 100 updated examples in this edition, with 42 new figures, plus improvements or updates to 20 existing figures. Dozens of new questions have been written to correspond to the new material and, in response to reviewers, many other questions have been re-written to focus more on concepts rather than specific examples. Several new terms have also been added in the text and glossary to increase student understanding and to reflect the evolving nature of the field. We have also continued to expand connections with evolution and global change in this edition.

Significant Chapter-by-Chapter Changes

Chapter 1 In response to reviewer's comments, we have created a new section that describes the different tools used by ecologists, introducing five new terms including *ex situ* and *in situ.* There are a total of nine new figures. We have revised figure 1 and added microbial ecology as an important frontier. We have added new examples from recent literature, including about evolution in alpine chipmunks. Questions were updated.

Chapter 2 Three new figures were added, including from research on habitat conversion in India. Data on tropical forest loss was updated. New examples from publications by women of color on soils and on logging of boreal forests were added. Wording in several places was clarified in response to reviewers' comments. An explanation of the distinction between weather and climate change was added. Improvements were made to 10 figures, including updating the drought data in figure 2.41 to 2020 and relating it to fires. Questions were updated.

Chapter 3 Six citations were updated. Sections added on United Nations Decade of Ocean Science, microplastics from research by Chatterjee and Sharma (2019), and updated several examples. One figure was updated with current global ice levels.

Chapter 4 The "applications" section was re-written with an updated example of herbicide resistance by Sushila Chaudhari and her colleagues, including a new figure. Questions were updated, and an existing figure improved.

Chapter 5 A total of 13 new citations, including examples with current citations were provided of how global warming is affecting ecosystems. New example and figure created to describe relationship between water temperature and canopy cover. Research on endothermic fish updated, with a new figure created and concept of RM endothermy added. Old example replaced with new section on comparisons between endothermic and ectothermic fish with research by a man of color, including another new figure. Questions were updated.

Chapter 6 Section on water-harvesting re-written with updated information and a new figure adapted from the review by Guera and Bhushan (2020). Added concept of cohesion, per reviewer request. Concepts hydrophilic and hydrophobic introduced. Water isotope section re-written to clarify per reviewer request, including a new figure to explain. Applications section was re-written with updated example from the meta-analysis by Evaristo and McDonnell (2017). Questions and one figure were updated.

Chapter 7 Information about chemosynthesis was expanded and updated with example from Naples, Italy. Peppered moth example re-written and figure replaced with one that shows actual photographs and data. Old predation examples were replaced with those using wolf spiders and coral reef fishes research from teams led by women, including new figures. Questions were updated.

Chapter 8 Opening photo replaced with a more appropriate one, six references updated. Section on nonrandom mating in plants significantly updated and clarified. Paragraph on phylogenies based on genetic analysis added. Updated number of cooperative breeding species. Updated section on lion cooperation with research by Natalia Borrego. Questions were updated.

Chapter 9 New example of gorillas replaces an old example, and new paragraph added based on the 2020 Living Planet Report. One new image. More information about the Breeding Bird Survey with updated references. Term endemic added, with paragraph replaced with new example of bird from Hawaii. Figure on rarity and vulnerability to extinction significantly improved in response to reviewer request. Questions were updated.

Chapter 10 Seven citations updated. Research on "killer" bees updated with genetics research led by a man of color, including updated figure. Added information and example of pumas in Patagonia to migration section. Questions updated.

Chapter 11 Introduction re-written with example from the COVID-19 pandemic, including new figures. Three figures updated, including one for current numbers of whooping cranes and another with human population growth. Questions were updated.

Chapter 12 Paragraph replaced with section on life history trade-offs, based on ideas by Anurag Agrawal. Updated number of species of fish with 2020 data from IUCN. One figure improved. Questions were updated.

Chapter 13 Self-thinning section updated with research from people of color, and new figure added to better explain zero growth isocline, per reviewer request. Existing Lotka-Volterra figure simplified. Competition meta-analysis research by Jessica Gurevitch and colleagues added. Extra example of competition deleted, per reviewer request. Questions updated.

Chapter 14 Section on research by Utida shortened and simplified per reviewer request, including an improvement to an existing figure. Questions were re-written to focus on concepts rather than specific research. Two citations updated.

Chapter 16 The concept of a species rarefaction curve is introduced. A new example of sampling benthic macroinvertebrates replaces an old example, work done by a man of color that also introduces the concept of DNA barcoding, including new figures. Questions were updated.

Chapter 17 Four examples were updated, all from research led by underrepresented scientists. This includes a new "Applications" example on hyperparasitoids with a new figure. Questions were updated.

Chapter 18 Section on primary productivity of oceans was re-written with updated environmental factors and relating this to global change. Map on marine primary productivity has been updated. Research on top-down vs. bottom-up updated with a new section and figure from meta-analysis research conducted by Mayra Vidal, a woman of color, and Shannon Murphy. Concept of tri-trophic interactions added. Eleven citations were updated, most of which from papers with underrepresented lead authors. Paragraph on role of microorganisms added, per reviewer request. Questions were updated.

Chapter 20 All sections on succession at Glacier Bay section completely re-written to reflect more current research led by Brian Buma that changes interpretation of those research, including new figures. This case study becomes a more interesting story about how understanding can evolve with new information. Questions were updated.

Chapter 21 Reference to the 2020 California wildfires was added, including a short paragraph about research from UC Berkeley. Questions were updated.

Chapter 23 A total of five new figures added, including one that refers to the Australian wildfires of 2020. Figure on atmospheric CO_2 updated with current values. Section on nitrogen pollution re-written with more explanation and more current research. The forest section was re-written with forest biodiversity data from the FAO 2020 report on the State of the World's Forests and other current research. Corrections made to use of Spanish words, per reviewer request. Deforestation in Brazil was updated. There were a total of 13 new citations, 9 from underrepresented scientists. Questions were updated.

Online Materials

Available online are suggested readings and answers to concept review, chapter review, and critiquing the evidence questions.

Related Title of Interest from McGraw-Hill Education

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

Darrell Vodopich, coauthor 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.

Acknowledgments

First and foremost, I must thank my academic partner Dr. Eduardo González, without whose help I could have never completed this edition. I am also deeply grateful for pedagogical expertise of Julie Morris, who also went above and beyond. Thanks also go to the other members of the Sher Lab who pitched in with research and/or offered feedback on new figures for the ninth edition, including Ali Alghamdi, Violet Butler, Rhys Daniels, Alex Goetz, Annie Henry, Alex Kim, Lily Malone, Mandy Malone, and Allen Williamson. During the development of this textbook, many colleagues freely shared their expertise, reviewed sections, or offered the encouragement a project like this needs to keep it going: Anurag Agrawal, Brian Buma, Candice Galen, Diane Marshall, Scott Nichols, Mayra Vidal, and Dhaval Vyas. I am grateful to Patrick M. Burchfield and Hector Chenge Alvarez for keeping me up to date in data and photos of turtles. Special thanks to Jake Grossman for sharing his list of Ecologists of Color and Indigenous Ecologists.

We would like to especially thank Shannon Murphy for her extensive suggestions for the ninth edition, as well as for providing us with exciting new case studies to illustrate evolutionary ecology concepts. In addition, we are indebted to the many students and instructors who have helped by contacting us with questions and suggestions for improvements.

We also wish to acknowledge the skillful guidance and work throughout the publishing process given by many professionals associated with McGraw-Hill Education and Straive during this project, including Beth Baugh, Melissa Homer, Jodi Rhomberg, and Mithun Kothandath.

We gratefully acknowledge the many reviewers who, over the course of the many revisions, have given of their time and expertise to help this textbook evolve to its present ninth edition. Note that some feedback that did not make it into this edition will be incorporated into the next one. These reviewers continue our education, for which we are grateful, and we honestly could not have continued the improvement of this textbook without them.

Finally, I would like to thank my co-author Manuel Molles for entrusting me with this wonderful series, as well as my wife Fran and our son Jeremy for their support throughout the production of the ninth edition.

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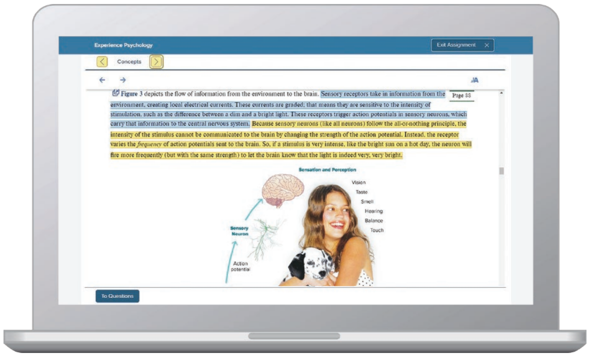

Figure 3 depicts the flow of information from the environment to the brain. Sensory receptors take in information from the environment, creating local electrical currents. These currents are graded; that means they are sensitive to the intensity of stimulation, such as the difference between a dim and a bright light. These receptors trigger action potentials in sensory neurons, which carry that information to the central nervous system. Because sensory neurons (like all neurons) follow the all-or-nothing principle, the intensity of the stimulus cannot be communicated to the brain by changing the strength of the action potential. Instead, the receptor varies the *frequency* of action potentials sent to the brain. So, if a stimulus is very intense, like the bright sun on a hot day, the neuron will fire more frequently (but with the same strength) to let the brain know that the light is indeed very, very bright.

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Chapter 1

Introduction to Ecology

Historical Foundations and Developing Frontiers

NPS Photo by Jeff Foott

A yellow-rumped warbler, *Dendroica coronata,* feeding young. Ecological studies of warblers have made fundamental contributions to the growth of ecological understanding.

CHAPTER CONCEPTS

LEARNING OUTCOME

After studying this section you should be able to do the following:

1.1 Discuss the concept of environment as it pertains to the science of ecology.

What is ecology? **Ecology** is the study of relationships among organisms and between organisms and the physical environment. These relationships influence many aspects of the natural world, including the distribution and abundance of organisms, the variety of species living together in a place, and the transformation and flow of energy in nature.

Humans are rapidly changing earth's environment, yet we do not fully understand the consequences of these changes. For instance, human activity has increased the quantity of nitrogen cycling through land and water, changed land cover across the globe, and increased the atmospheric concentration of CO_2. Changes such as these threaten the diversity of life on earth and will also endanger our life support system. Because of the rapid pace of environmental change in the early twenty-first century, it is imperative that we better understand earth's ecology.

Behind the simple definition of ecology lies a broad scientific discipline. Ecologists may study individual organisms, entire forests or lakes, or even the whole earth. The measurements made by ecologists include counts of individual organisms, rates of reproduction, and rates of processes such as photosynthesis and decomposition. Ecologists often spend as much time studying nonbiological components of the environment, such as temperature and soil chemistry, as they spend studying organisms. Meanwhile, the "environment" of organisms in some ecological studies is other species. While you may think of ecologists as typically studying in the field, some of the most important conceptual advances have come from ecologists who build theoretical models or do ecological research in the laboratory. Clearly, our simple definition of *ecology* does not communicate the great breadth of the discipline or the diversity of its practitioners. To get a better idea of what ecology is, let's briefly review its scope.

1.1 Overview of Ecology

LEARNING OUTCOMES

After studying this section you should be able to do the following:

1.2 Describe the levels of ecological organization, for example, population, studied by ecologists.
1.3 Distinguish between the types of questions addressed by ecologists working at different levels of organization.
1.4 Explain how knowledge of one level of ecological organization can help guide research at another level of organization.

Ecologists study environmental relationships ranging from those of individual organisms to factors influencing global-scale processes. This broad range of subjects can be organized by arranging them as levels in a hierarchy of ecological organization, such as that embedded in the brief table of contents and the sections of this book. Figure 1.1 attempts to display such a hierarchy graphically.

Historically, the ecology of individuals, (fig. 1.1A), has been the domain of physiological ecology and behavioral ecology. Physiological ecologists have emphasized the **evolution** (a process by which populations change over time) of physiological and anatomical mechanisms by which organisms adapt to challenges posed by physical and chemical variation in the environment. Meanwhile, behavioral ecologists have focused principally on evolution of behaviors that allow animals to survive and reproduce in the face of environmental variation.

There is a strong conceptual linkage between ecological studies of individuals and of populations particularly where they concern evolutionary processes. Population ecology is centered on the factors influencing population structure and process, where a **population** is a group of interbreeding individuals of a single species inhabiting a defined area (fig. 1.1B). The processes studied by population ecologists include adaptation, extinction, the distribution and abundance of species, population growth and regulation, and variation in the reproductive ecology of species. Population ecologists are particularly interested in how these processes are influenced by nonbiological and biological aspects of the environment.

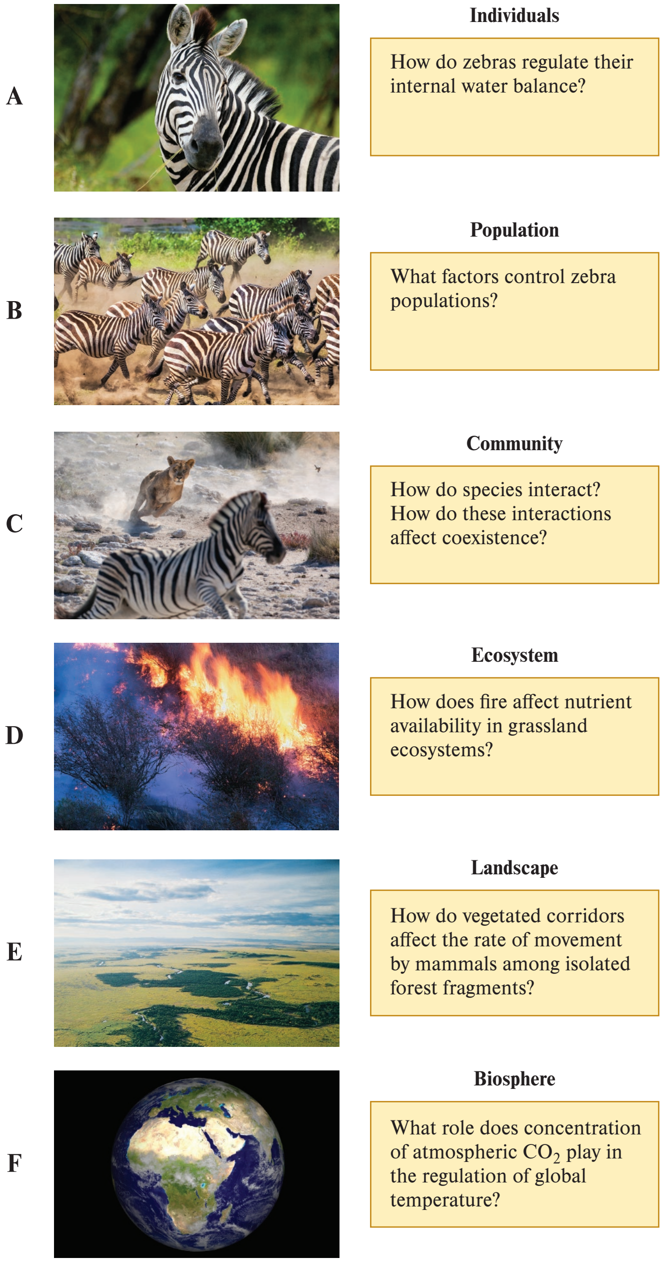


Figure 1.1 Levels of ecological organization and examples of the kinds of questions asked by ecologists working at each level. These ecological levels correspond broadly to the sections of this book.
(*A*) Glow Images; (*B*) cinoby/E+/Getty Images; (*C*) Mogens Trolle/Shutterstock; (*D*) Photo by Gary Wilson, USDA Natural Resources Conservation Service; (*E*) Comstock/PunchStock; (*F*) Calysta Images/Getty Images

Bringing biological components of the environment into the picture takes us to the next level of organization, the community (fig. 1.1C). A **community** is an association of interacting species. Ecologists who study interactions between species have often emphasized the evolutionary effects of the interaction on the species involved. Other approaches explore the effect of interactions on population structure or on properties of ecological communities.

The next level of organization is the **ecosystem.** An ecosystem is a biological community together with its associated physical and chemical environment. Community and **ecosystem** ecology have a great deal in common, since both are focused on multispecies systems. However, the objects of their study differ. While community ecologists concentrate on understanding environmental influences on the kinds and diversity of organisms inhabiting an area, ecosystem ecologists focus on ecological processes such as energy flow and decomposition (fig. 1.1D).

To simplify their studies, ecologists have long attempted to identify and study isolated communities and ecosystems. However, all communities and ecosystems on earth are subject to exchanges of materials, energy, and organisms with other communities and ecosystems. The study of these exchanges, especially among ecosystems, is the intellectual territory of **landscape** ecology (fig. 1.1E). Landscape ecology in turn leads us to the largest spatial scale and highest level of ecological organization—the **biosphere,** the portions of the earth that support life, including the land, waters, and atmosphere (fig. 1.1F).

While this description of ecology provides a brief preview of the material covered in this book, it is a rough sketch and highly abstract. To move beyond the abstraction represented by figure 1.1, we need to connect it to the work of the scientists who have created the discipline of ecology. To do so, let's briefly review the research of ecologists working at a broad range of ecological levels emphasizing links between historical foundations and some developing frontiers (fig. 1.2).

Concept 1.1 Review

1. How does the level of ecological organization an ecologist studies influence the questions he or she poses?
2. While an ecologist may focus on a particular level of ecological organization shown in figure 1.1, might other levels of organization also be relevant? For example, why should an ecologist studying factors limiting numbers in a population of zebras consider the influences of interactions with other species or the influences of global processes such as climate change?

1.2 Sampling Ecological Research

LEARNING OUTCOMES

After studying this section you should be able to do the following:

1.5 List three categories of ecological research, and give an example of each.

1.6 Explain how new tools and technology can be used to advance each category of ecological research.

1.7 Describe different types of ecological models and explain how are they used.

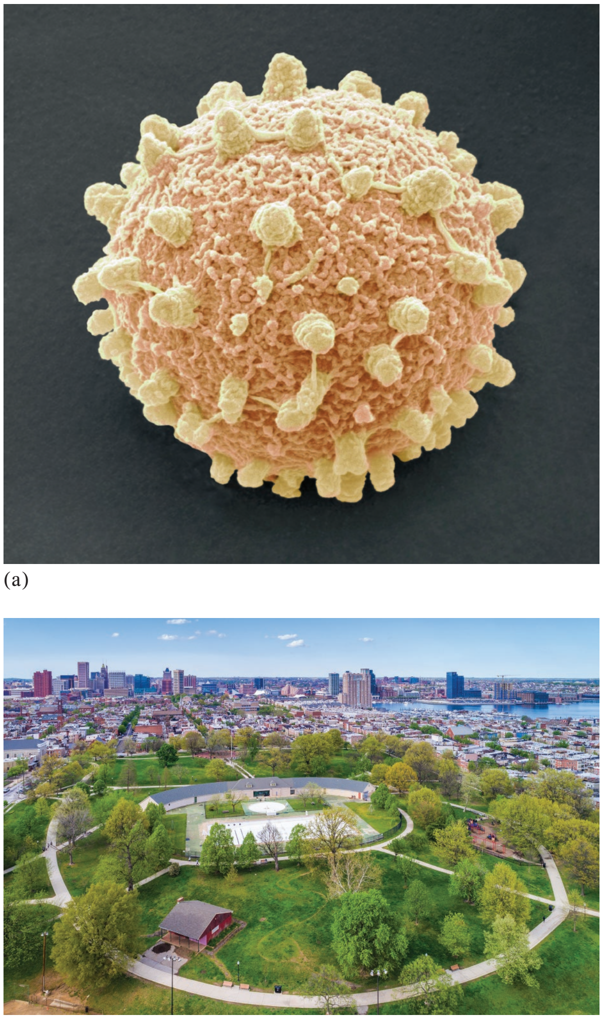


Figure 1.2 Two rapidly developing frontiers in ecology. (*a*) **Microbial ecology:** the study of the interactions among microorganisms and between them and their environment (e.g., Epps and Arnold 2019). The importance of these organisms for regulating systems from populations to ecosystems is becoming increasingly understood. (*b*) **Urban ecology:** the study of urban areas as complex, dynamic ecological systems, influenced by interconnected, biological, physical, and social components. As ecologists focus their research on the environment where most members of our species live, they have made unexpected discoveries about the ecology of urban centers such as the city of Baltimore (see chapter 19). (*a*) STEVE GSCHMEISSNER/Science Photo Library/Getty Images; (*b*) Jon Bilous/Shutterstock

Ecologists design their studies based on their research questions, the temporal and spatial scale of their studies, and available research tools. Because the discipline is so broad, ecological research can draw from all the physical and biological sciences. The following section of this chapter provides a sample of ecological questions and approaches to research.

Types of Research

In the broadest sense, we can consider ecological research in three general categories: observation, experimentation, and modeling. Each of these types of research is necessary for understanding the organisms and processes at work in our world; most ecologists use at least two, if not all three approaches to answer ecological questions.

Observation

Observation refers to the collection of data in unmanipulated settings, such as counting numbers of birds in a patch of forest or describing types of fungal spores seen through a microscope. Some of this work takes place in the field, or ***in situ,*** meaning in the habitat where the organisms live, while other research uses specimens that have been collected in the field but are observed in a laboratory or other setting. Such specimens may have been sampled for that specific purpose or may have been collected long beforehand and stored for future study, such as those found in an herbarium or museum. For example, many researchers have been able to track the impact of climate change on plant communities using thousands of plant specimens collected over more than a century (Jones and Daehler 2018, Piao et al. 2019). Observational research can be purely descriptive or may test a hypothesis, such as to understand relationships between organisms. This may involve comparing observations over time or space.

An important, historical example of ecological observational research is that by Robert MacArthur, who observed warblers in spruce forests of northeastern North America (MacArthur 1958). Theory had predicted that two species with identical ecological requirements would compete with each other and that, as a consequence, they would not live in the same environment indefinitely. MacArthur wanted to understand how several warbler species with apparently similar ecological requirements could live together in the same forest; by observing the birds in their natural habitat, he determined that each warbler species had a distinct feeding zone (fig. 1.3). He concluded that this partitioning of the tree reduced competition among the warblers, stimulating future generations of studies of competition.

Another classic example of observational research is the work by Nalini Nadkarni (1981, 1984a, 1984b), who changed our ideas of how tropical and temperate rain forests are structured and how they function. Nadkarni was one of the first scientists to study the ecology of the unseen world of the forest canopy (fig. 1.4). Using mountain-climbing equipment, she took inventories of the distribution of nutrients in rain forests in both Costa Rica and the Pacific Northwest of the United States. She discovered through this sampling that as much as four times the nutrient content in trees leaves was found in **epiphytes**—plants such as orchids, ferns, and mosses that grow on the tree trunks and branches.

MacArthur's primary research tool was a pair of binoculars and Nadkarni's was ropes and harness; however, today there are many more means by which we can collect observational data. For example, new ways to access the forest canopy range from hot air balloons and large cranes (see Investigating the Evidence 16 in Appendix A) to unmanned aerial vehicles (UAV) such as drones. These can carry cameras and other equipment to collect data (Waite et al. 2018). Thermal sensors on UAV's have been used to survey animals in the treetops at night (Kays et al. 2019).

Another example of a new type of data being collected is stable isotope analysis (see chapter 6). Isotopes of a chemical element, such as isotopes of carbon, have different atomic masses as a result of having different numbers of neutrons. Water and nutrients from different sources can have different

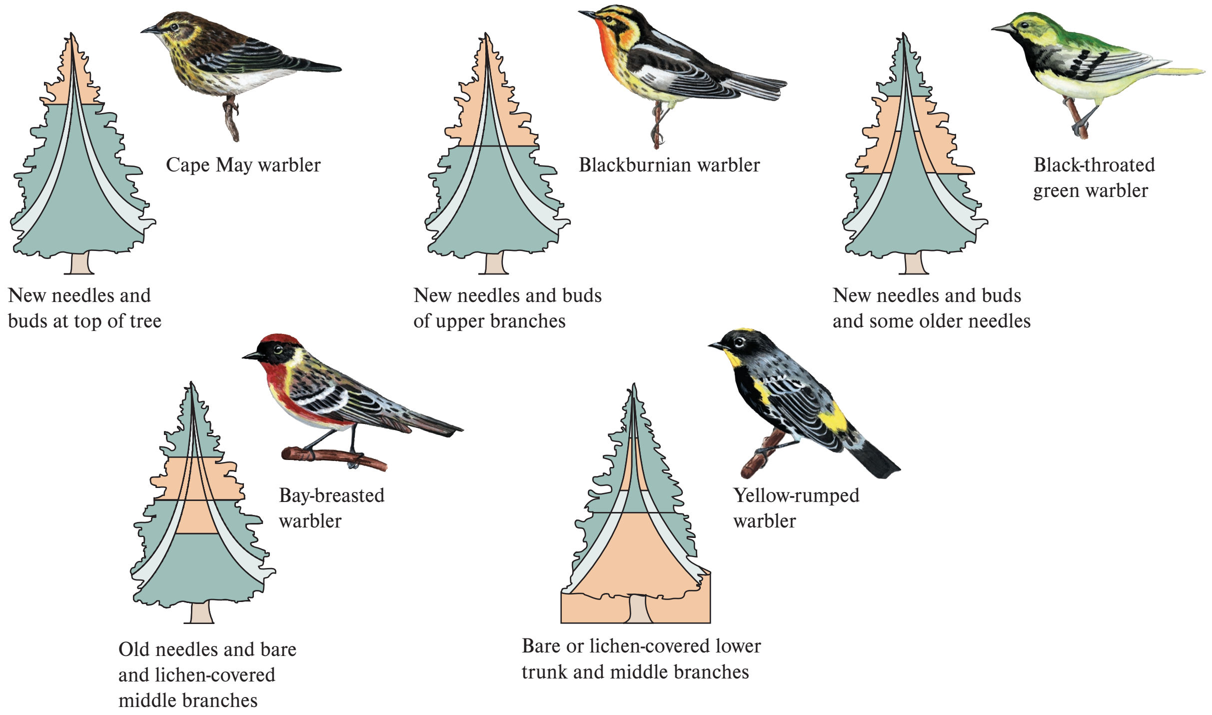


Figure 1.3 Warbler feeding zones shown in beige. The several warbler species that coexist in the forests of northeastern North America feed in distinctive zones within forest trees.

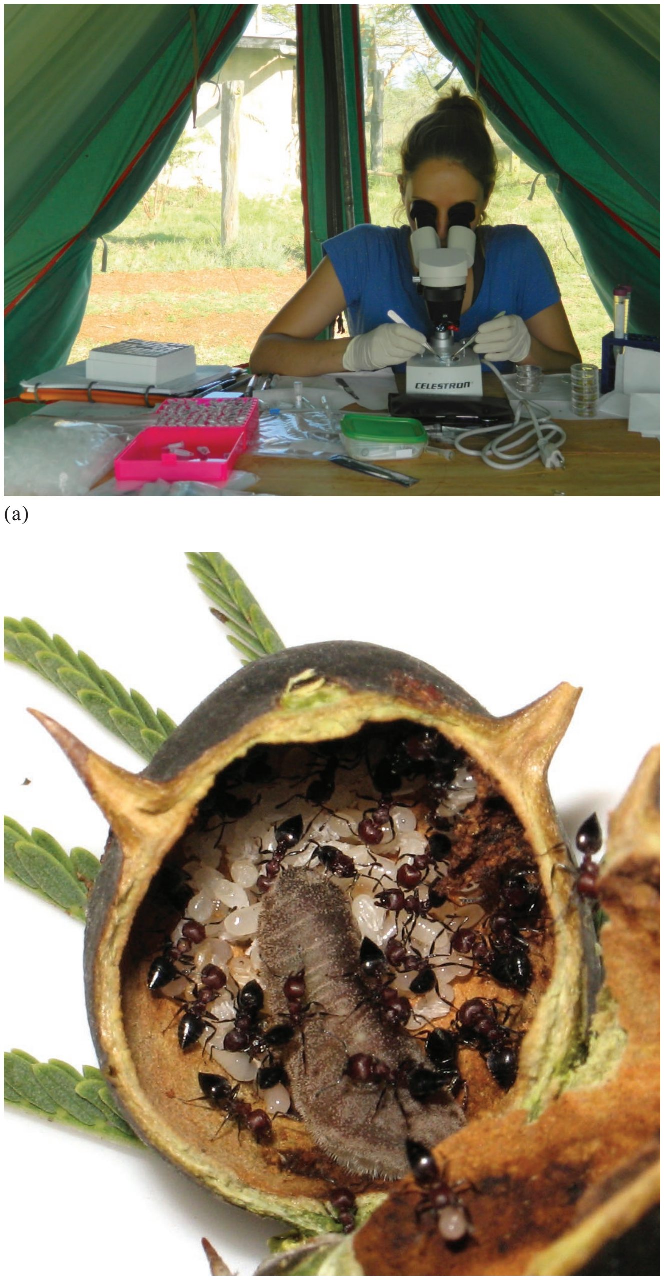
Figure 1.4 Exploring the rain forest canopy. What Nalini Nadkarni discovered helped solve an ecological puzzle. Courtesy Nalini Nadkarni, photo by Dennis Paulson

isotopic signatures, thus allowing us to trace them through ecosystems. In this way, stable isotope analysis provides ecologists with a new type of "lens" capable of revealing ecological relationships that would otherwise remain invisible. Melissa Whitaker and colleagues used both stable isotope and genetic analysis to identify trophic relationships for the *Anthene usamba,* a butterfly whose larval stage is found on whistling thorn acacia trees (*Vachellia drepanolobium*) (Whitaker et al. 2019). For this species, like many small organisms, there were no direct observations of feeding behavior in the field. However, because they were found on acacia trees that have a mutualism with ants, it was hypothesized that the butterfly larvae might feed upon regurgitations from ants or even eat ants themselves. By analyzing the DNA and nitrogen isotope signatures of the gut contents of butterfly larvae at field sites on Suyian Ranch in Laikipia County, Kenya (fig. 1.5*a*). Whitaker's group determined that these *A. usamba* larvae were, in fact, herbivorous, feeding almost exclusively off of the acacia tree itself (fig. 1.5*b*).

All of these examples are considered observational studies because there was no manipulation of variables in the field; data were collected on organisms as they existed in their natural environment.

Experimentation

While observational research is critically important for the field of ecology because it allows us to define patterns in nature, it is limited because observation cannot be used to definitively exclude a possible phenomenon (Tilman 1989). That is, just because we have never observed something (like a butterfly eating an ant) is not enough to say it is theoretically impossible. This is why **experiments** may also be necessary. Experimentation typically refers to research that involves manipulation of variables of interest while holding others



(a)

(b)

Figure 1.5 (*a*) Observational research in Kenya, East Africa, by Melissa Whittaker and colleagues on the African lycaenid butterfly, *Anthene usamba.* Since the larvae of the butterfly were found in acacia tree galls with ants (*b*), it had been hypothesized that it ate ant excretions. However, isotope research found that this was incorrect; because acacia leaves have a particular nitrogen isotope signature, researchers were able to identify it in the gut of the butterfly's larvae. (*a*) Julianne Pelaez; (*b*) Dino Martins constant in order to test a hypothesis. In her book co-authored with Elizabeth Lunbeck about scientific observation, Lorraine Daston described the relationship between observational research and experiments thus:

> *"Observation, by the curiosity it inspires and the gaps that it leaves, leads to experiment; experiment returns to observation by the same curiosity that seeks to fill and close the gaps still more; thus one can regard experiment and observation as in some fashion the consequence and complement of one another" (Datson 2011)*

Experiments can occur in the field or in a more controlled setting, such as in a lab, garden, greenhouse, or outdoor enclosures for animals. Ecological experimentation in the field can be difficult to interpret because of the number of factors that may influence the data being collected, including factors that may be unknown to the researcher. In contrast, ***ex situ*** (not in the natural environment) experimentation has the benefit of being able to exclude all but the factors of interest in the experiment; however, it has the limitation of not representing real life. Both *ex situ* and *in situ* observation and experimentation may be necessary to fully understand the ecology of an organism or system.

In a classic example of experimentation, Candace Galen tested the importance of bees for the evolution of the alpine wildflower *Polemonium viscosum* growing on Pennsylvania Mountain, Colorado (fig. 1.6*a*). Observational research had suggested that bumblebees prefer larger flowers, and also that more visitation by bees meant more pollen transferred and thus more seeds produced. More seeds means greater fitness. But it was also possible that some other factor such as nutrients produced both big flowers and lots of seeds in some plants. Were the bees important for the evolution of flower size? Galen was one of the first to experimentally test the hypothesis that larger flowers would have more seeds specifically because they were more attractive to bees (Galen 1989). To do this, she compared seed set in plants that were exposed to pollination by bumblebees (the treatment) versus plants that were hand-pollinated and bagged to exclude bees (the control). Both groups included plants with a range of flower sizes. She found that seed number significantly increased with flower size when pollinated by bees (fig. 1.6b), but that flower size did not predict seed number in the control group. That is, her experiment showed that not only did bees prefer larger flowers, but also that the bees were influencing the evolution of larger flowers because they caused those plants to have greater fitness.

As with observational research, new tools and technology have also advanced ecological experimentation. More than 30 years after her groundbreaking work on bumblebee pollination, Galen is still researching the ecology and evolution of these systems, most recently using a newly developed tool for analyzing audio recordings of bees' wing movements. Galen and her colleagues took advantage of a **natural experiment** created by a solar eclipse to investigate the impact of light and temperature on bees' behavior (Galen et al. 2019). They were able to compare behavior during darkness (the treatment created by the eclipse) to daylight (the control) within a single hour by detecting bee movements using their sound. In order to obtain a very large sample over a wide geographic area, they used another new resource: data collected by non-scientists. School children and other "**citizen scientists**" assisted in collecting recordings of bees' buzzing at 11 locations in 3 regions using tiny USB microphones dispersed among flowers (fig. 1.7*a*). Recordings of the bees buzzing were then digitally analyzed to document the dramatic decrease in bee movement during the eclipse (fig. 1.7*b*). Statistical analysis was used to determine that this decrease was due primarily to light, rather than temperature.

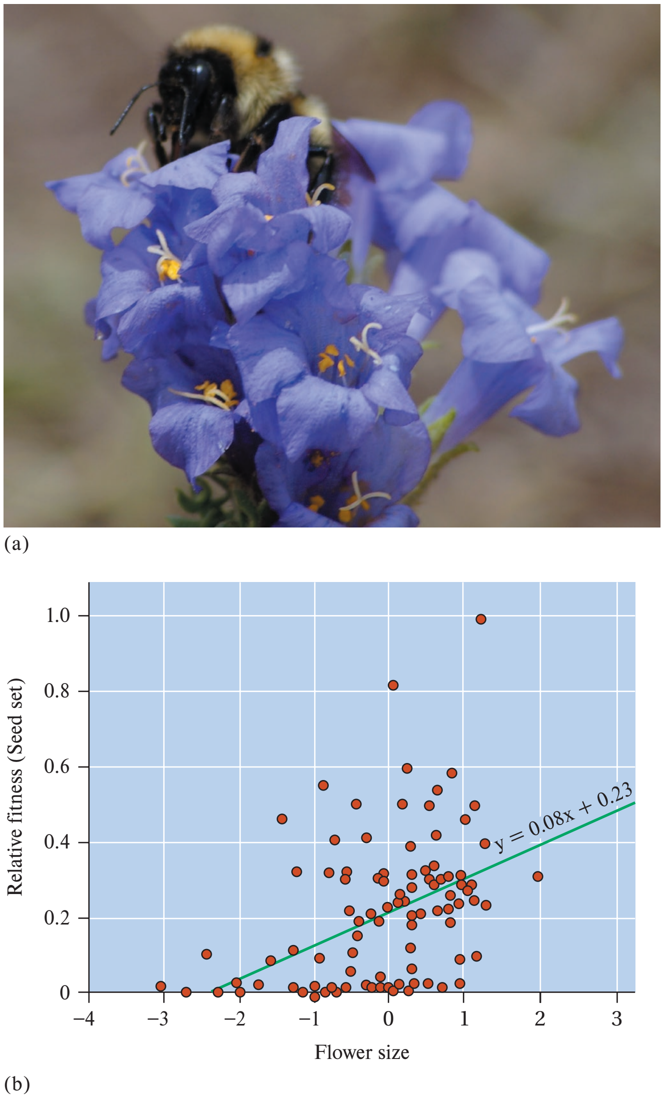


Figure 1.6 Experimental research on *Polemonium viscosum,* an alpine flower in Colorado, USA (*a*), demonstrated that increasing flower size was positively associated with fitness, as measured by seed set, in flowers pollinated by bumblebees. (*b*) We know that bumblebees are driving this relationship because no such relationship was found for flowers that were hand-pollinated (the control in the experiment) (the graph is adapted from Galen 1989). (*a*) Candace Galen

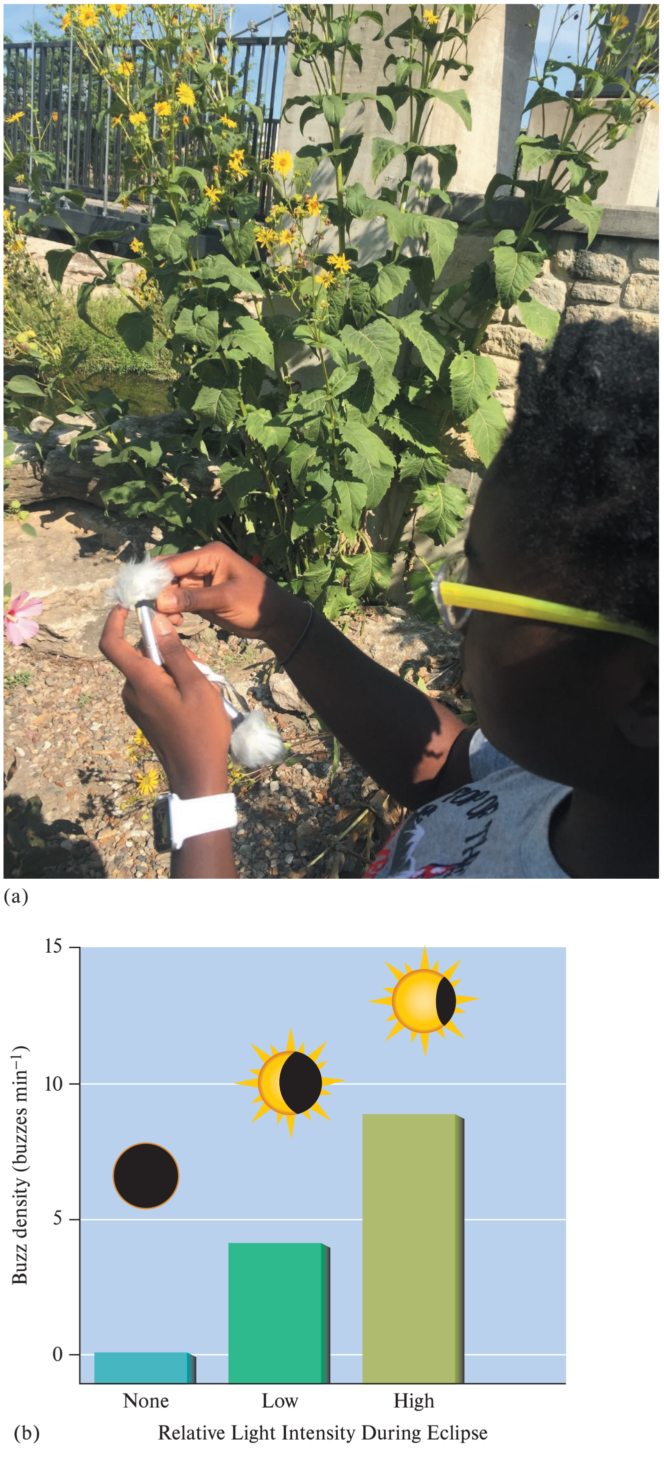


Figure 1.7 (*a*) Emilia Asante, a graduate student at the University of Missouri, assembles a microphone to record the buzzing of bees. The white, furry "jacket" screens out wind noise. (*b*) Recordings of the bees buzzing documented a dramatic decrease in bee activity as measured by buzz density during the eclipse. (*a*) Candice King; (*b*) adapted from Galen et al. 2019

Modeling

Modeling is the creation and analysis of representations of data or ideas to provide insight or make predictions. In ecology, models usually represent a hypothesis regarding how a system works. **Conceptual models** are those which describe systems in pictures or diagrams, whereas **quantitative models** are mathematical and may involve complex equations. Like observational research, models can be purely descriptive can be designed to test a hypothesis. A line, which can be represented by the equation $y = mx + b$, is an example of a very simple quantitative model that has many applications within ecology. In Galen's early work, a line could be used to represent the relationship between flower size and fitness (fig. 1.6*b*). The line does not explain all of the variability in fitness, but it does generally define the rate at which seed set increases with increasing flower size. In this way, a model can be a tool used by ecologists to understand the data they have collected. In other cases, modeling may describe or predict patterns using data from published work by others. In chapter 6, we will learn about a modeling approach that is used to summarize findings from many different studies at once.

Models may also be used to represent a novel hypothesis that can then be tested with or compared against future observational or experimental data. In chapter 22, we will learn about McArthur and Wilson's Island Biogeography model; this is a conceptual model based on observed data to explain how size of islands and their proximity to the mainland affect species diversity. This model has been applied to many species and ecosystems, and it has even helped us understand the dynamics of protected areas as land-islands (Sher and Primack 2018).

Finally, models can be used to simulate natural systems, allowing us to test scenarios that would be too difficult, expensive, or logistically impossible to do in real life. For example, Annette Janssen and others created a computer program that can be used to predict growth of algae in lake ecosystems, based on different climate models (Janssen et al. 2019). Janssen's model includes multiple ecological feedbacks that affect algal growth in deep lakes, making it possible to quantify how the lake will respond to different nutrient levels under climate warming. The mathematical equations involved in creating the simulations can be represented by a conceptual model (fig. 1.8). Although the Janssen et al. model may seem complex, many mathematical simulations of this type are even more so in their attempt to represent the real world. Such simulations are important for understanding what has both happened in the past as well as what may happen in the future.

Climatic and Ecological Change: Past and Future

The earth and its life are always changing. However, many of the most important changes occur over such long periods of time or at such large spatial scales that they are difficult to study. Two approaches that provide insights into long-term and large-scale processes are studies of pollen preserved in lake sediments and of evolutionary change.

Margaret B. Davis (1983, 1989) carefully searched through a sample of lake sediments for pollen. The sediments had come from a lake in the Appalachian Mountains, and the pollen they contained would help her document changes in

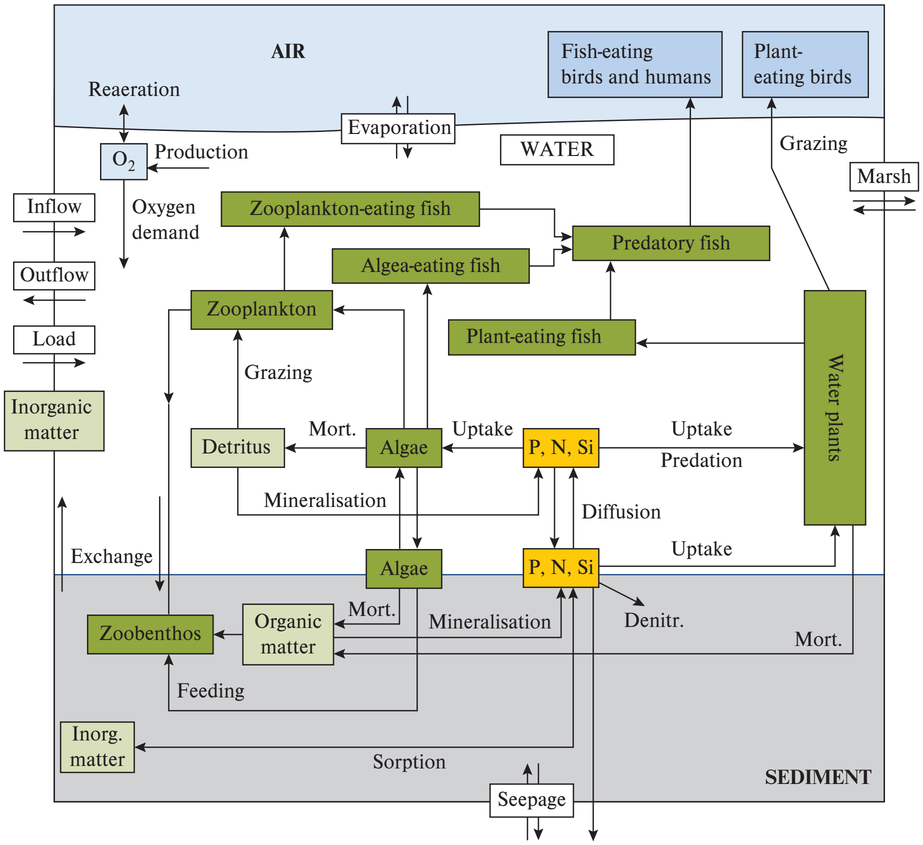


Figure 1.8 Ecological modeling research includes creating complex mathematical simulations of systems as a way of making predictions. Arrows indicate movement of energy or matter. This conceptual model or schematic of a lake ecosystem represents only a portion of a larger, a process-based mathematical model that was created to predict algal blooms under different environmental conditions (diagram based on Janssen et al. 2019).

the community of plants living near the lake during the past several thousand years. Davis is a paleoecologist trained to think at very large spatial scales and over very long periods of time. She has spent much of her professional career studying changes in the distributions of plants during the Quaternary period, particularly during the most recent 20,000 years.

Some of the pollen produced by plants that live near a lake falls on the lake surface, sinks, and becomes trapped in lake sediments. As lake sediments build up over the centuries, this pollen is preserved and forms a historical record of the kinds of plants that lived nearby. As the lakeside vegetation changes, the mix of pollen preserved in the lake's sediments also changes. In the example shown in figure 1.9, pollen from spruce trees, *Picea* spp., first appears in lake sediments about 12,000 years ago; then pollen from beech, *Fagus grandifolia,* occurs in the sediments beginning about 8,000 years ago. Chestnut pollen does not appear in the sediments until about 2,000 years ago. The pollen from all three tree species continues in the sediment record until about 1920, when chestnut blight killed most of the chestnut trees in the vicinity of the lake. Thus, the pollen preserved in the sediments of lakes can be used to reconstruct the history of vegetation in the area. Margaret B. Davis, Ruth G. Shaw, and Julie R. Etterson reviewed extensive evidence that during climate change, plants evolve, as well as disperse (Davis and Shaw 2001; Davis, Shaw, and Etterson 2005). As climate changes, plant populations simultaneously change their geographic distributions and undergo the evolutionary process of **adaptation,** which increases their ability to live in the new climatic regime. Meanwhile, evidence of evolutionary responses to climate change has been found in many animal groups. One such example is evidence of rapid evolution in alpine chipmunks (*Tamias alpinus*) for a gene associated with high elevation stress (fig 1.10). This was discovered by researchers at the Museum of Vertebrate Zoology at the University of California using DNA from historic specimens (Bi et al. 2019). Evolution of adaptations to elevation have been shown in other rodents using field collected animals (Velotta et al. 2020).

In the remainder of this book, we will fill in the details of the sketch of ecology presented in this chapter. This brief survey has only hinted at the conceptual basis for the research described. Throughout this book we emphasize the conceptual foundations of ecology. We also explore some of the applications associated with the focal concepts of each chapter. Of course, the most important conceptual tool used by ecologists is the scientific method (see Investigating the Evidence 1 in Appendix A).

We continue our exploration of ecology in section I with natural history and evolution. Natural history is the foundation on which ecologists build modern ecology for which

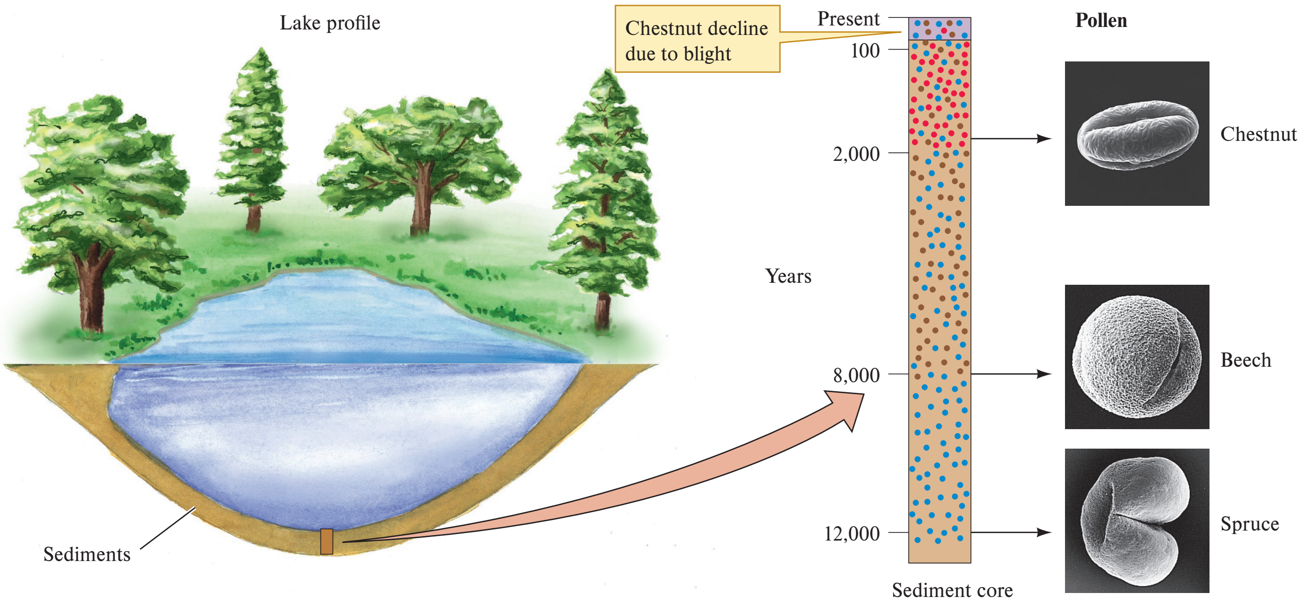


Figure 1.9 The vegetation history of landscapes can be reconstructed using the pollen contained within the sediments of nearby lakes. (Chestnut, Beech and Spruce) Courtesy of the Gretchen and Stanley Jones Palynological Collection and the Botanical Research Institute of Texas

Figure 1.10 Studies indicate that alpine squirrels (*Tamias alpinus*) are evolving adaptations to higher elevations (Bi et al. 2019). Danita Delimont/Getty Images

evolution provides a conceptual framework. A major premise of this book is that knowledge of natural history and evolution improves our understanding of ecological relationships.

Concept 1.2 Review

1. What characterizes each of the three types of ecological research? How are they different and how might they be used together?
2. What are some of the new tools and technology being used in ecological research? Why are they valuable?
3. How are ecologists able to look backwards and forwards in time? Why is this important?

Applications

Ecology Can Inform Environmental Law and Policy

LEARNING OUTCOMES

After studying this section you should be able to do the following:

1.8 Describe the purposes of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the U.S. Endangered Species Act (ESA).

1.9 Discuss how subject areas covered in this text are applicable to identifying and managing endangered species.

Because ecological science concerns relationships between organisms and the environment, it is natural to turn to ecology when environmental concerns arise. Consequently, ecology has contributed prominently to the development of environmental law and policy. For example, ecologists have been essential to evaluating the effects of pollution on the diversity of species in terrestrial and aquatic communities and on the functioning of ecosystems. One area where ecology has played a particularly significant role is in evaluating the status of individual species threatened by human impacts on the environment.

Ecological studies of animal and plant populations are essential to determining when species populations have declined in numbers to the point where they are in danger of extinction (see chapter 9). Reports of such declines in the 1960s eventually led to the establishment of international treaties and national laws to protect endangered species. Two prominent protections came into force in 1973. The first was the Convention on