Ecology

CONCEPTS & APPLICATIONS

Eighth Edition

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McGraw Hill Education

ECOLOGY: CONCEPTS AND APPLICATIONS, EIGHTH EDITION

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This book is printed on acid-free paper.

1 2 3 4 5 6 7 8 9 LMN 21 20 19 18

ISBN 978-1-259-88005-6
MHID 1-259-88005-2

Portfolio Manager: *Justin K. Wyatt, PhD*
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Cover Image: ©*Johner Images/Getty Images*
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Library of Congress Cataloging-in-Publication Data

Names: Molles, Manuel C., Jr., 1948– author.
Title: Ecology : concepts and applications / Manuel C. Molles Jr., University of New Mexico.
Description: Eighth edition. | New York, NY : McGraw-Hill Education, 2019. | Includes bibliographical references and index.
Identifiers: LCCN 2017046086 | ISBN 9781259880056 (alk. paper)
Subjects: LCSH: Ecology.
Classification: LCC QH541 .M553 2019 | DDC 577—dc23 LC record available at https://lccn.loc.gov/2017046086

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About the Authors

Courtesy of Manuel Molles

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 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. She was a double major in Biology and Art at Earlham College, where she has also taught ecology as a Howard Hughes Fellow, visiting lecturer, and as the co-leader of the Earlham Study Abroad Kenya Program in 1992, 2000, and 2002. 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.

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 coauthor of the textbook *An Introduction to Conservation Biology,* First Edition (Primack and Sher 2016). 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.

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Dedication

To Mary Anne
–Manuel C. Molles Jr.
To my wife Fran and our son Jeremy
–Anna A. Sher

Brief Contents

Design elements: (bat and cactus flower): ©Johner Images/Getty Images

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Section II
ADAPTATIONS TO THE ENVIRONMENT

Section III
POPULATION ECOLOGY

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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.

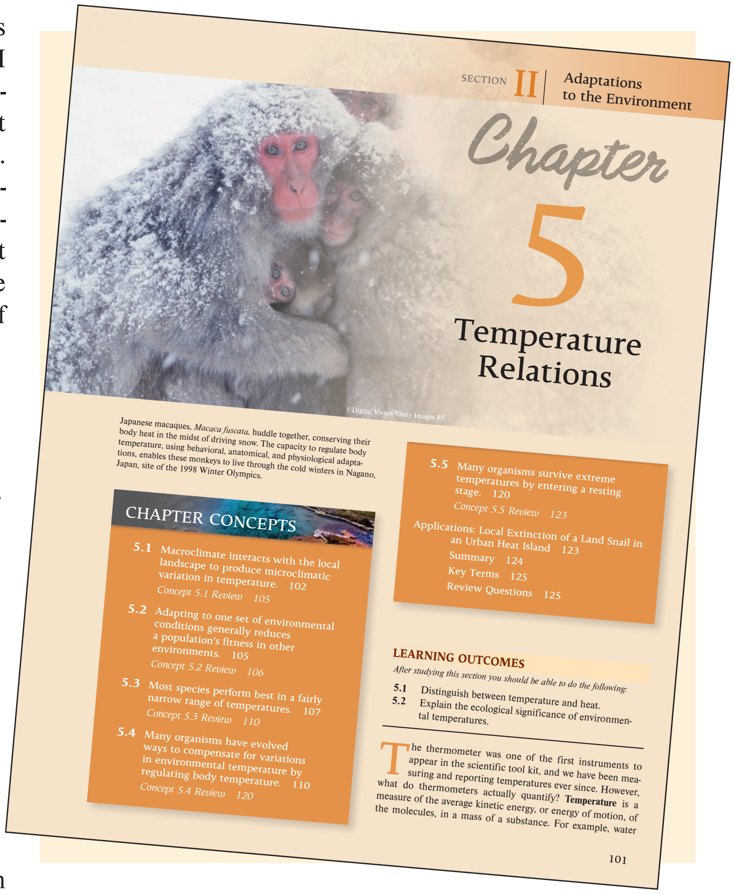
Features Designed with the Student in Mind

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 eighth 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

5.1 Macroclimate interacts with the local landscape to produce microclimatic variation in temperature. 102
Concept 5.1 Review 105

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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5.5 Many organisms survive extreme temperatures by entering a resting stage. 120
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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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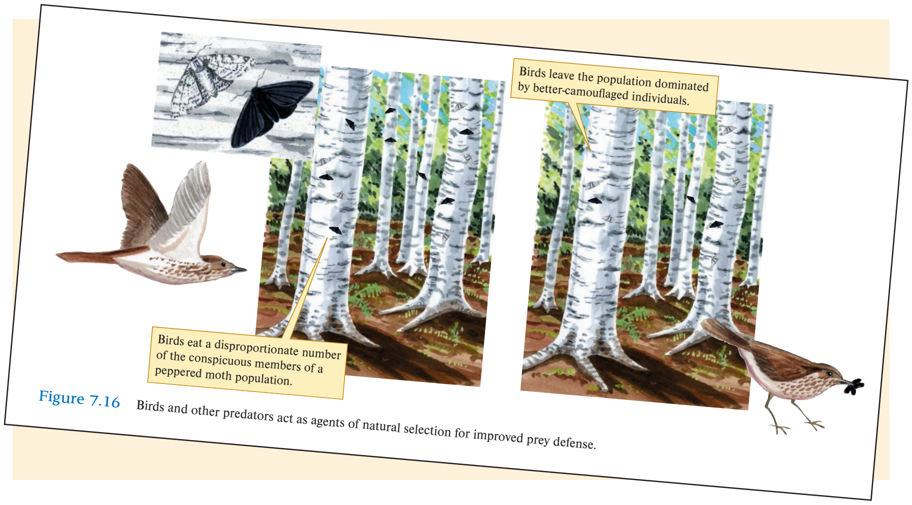
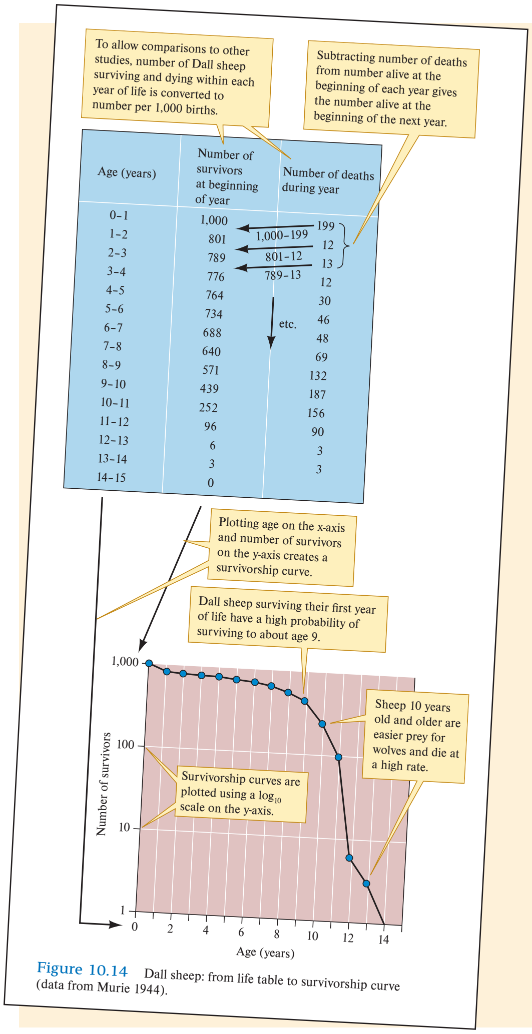
Illustrations: A great deal of effort has been put into the development of illustrations, both photographs and line art. The goal has been to create more-effective pedagogical tools through skillful design and use of color, and to rearrange the traditional presentation of information in figures and captions. 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.

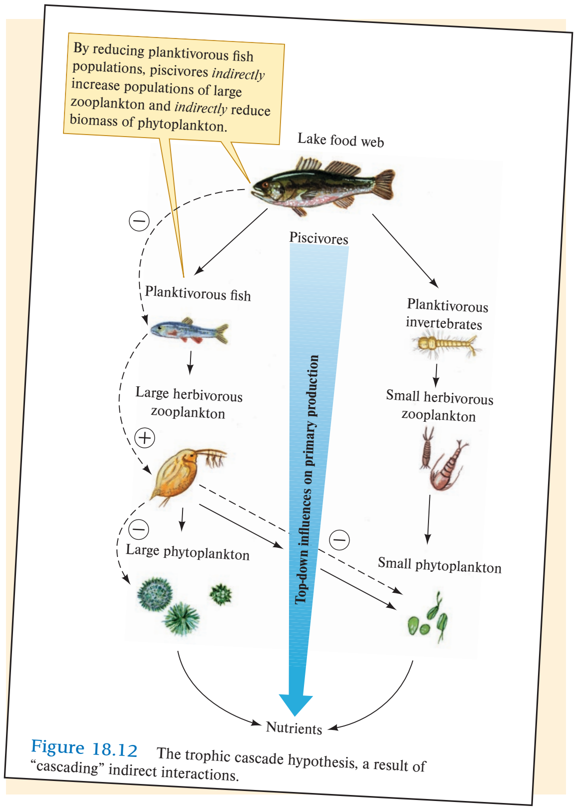


Visualizing a process involving a predator and its prey.



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	

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



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.
- ***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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Investigating the Evidence 16

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 Evidence box 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.

Critiquing the Evidence 16

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?


Chapter 9 Population Distribution and Abundance 211

Applications

Rarity and Vulnerability to Extinction

LEARNING OUTCOMES

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

9.15 List the seven forms of rarity described by Rabinowitz.

9.16 Detail examples of organisms showing each form of rarity described by Rabinowitz.

9.17 Explain the relationship between the forms of rarity and the vulnerability of species to extinction.

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 starlings, 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.

Ecologists exploring the relationship between size of geographic range and population size have found that they are not independent. Instead, there is a strong positive correlation between the two variables for most groups of organisms. In other words, species abundant in the places where they occur are generally widely distributed within a region, continent, or ocean, whereas species living at low population densities generally have small, restricted distributions. The positive relationship between range and population density was first brought to the attention of ecologists by Ilka Hanski (Hanski 1982) and James H. Brown (Brown 1984). Kevin Gaston (Gaston 1996; Gaston et al. 2000) points out that in the two decades since the early work by Hanski and Brown, ecologists have found a positive relationship between range and population density for many groups, including plants, grasshoppers, scale insects, hoverflies, bumblebees, moths, beetles, butterflies, birds, frogs, and mammals. Several mechanisms have been proposed to explain the positive relationship between local abundance and range size. Many of the explanations focus on breadth of environmental tolerances and differences in population dynamics. However, as Gaston and his colleagues point out (Gaston et al. 2000), there is still no consensus on the most likely explanations.

Most species are uncommon; seven combinations of range, tolerance, and population size each create a kind of rarity. As a consequence, Rabinowitz referred to "seven forms of rarity." Let's look at species that represent the two extremes of Rabinowitz's seven forms of rarity. The first two discussions concern species that are rare according to only one attribute. These are species that, before they become extinct, may seem fairly secure. The final discussion concerns the rarest species, which show all three attributes of rarity. Though these rarest species are the most vulnerable to extinction, rarity in any form appears to increase vulnerability to extinction.

Rarity I: Extensive Range, Broad Habitat Tolerance, Small Local Populations

It is easy to understand how people were drawn to the original practice of falconry. The sight and sound of a peregrine falcon, *Falco peregrinus,* in full dive at over 200 km per hour must have been one of the great experiences of a lifetime (fig. 9.23). The peregrine, which has a geographic range that circles the Northern Hemisphere and broad habitat tolerance, is uncommon throughout its range. Apparently, this one attribute of rarity was enough to make the peregrine vulnerable to extinction. The falcon's feeding on prey containing high concentrations of DDT, which produced thin eggshells and nesting failure, was enough to drive the peregrine to the brink of extinction. Peregrine falcons were saved from extinction by restricting the use of DDT, strict regulation of the capture of the birds, captive breeding, and reintroduction of the birds to areas where local populations had become extinct.

The range of the tiger, *Panthera tigris,* once extended from Turkey to eastern Siberia, Java, and Bali and included environments ranging from boreal forest to tropical rain forest. The tigers in this far-flung population varied enough from place to place in size and coloration that many local populations were described as separate subspecies, including the Siberian, Bengal, and Javanese tigers. Like peregrine falcons, tigers had an extensive geographic range and broad habitat tolerance but low

New to the Eighth Edition

Chapters 2 and 3 have been edited to incorporate a more holistic view and to better integrate them with later chapters. We have revised text and provided seven new figures and several revisions of existing figures to address requests by reviewers to expand the explanations of the relationships between abiotic features and biome type. The introductions to these chapters have been rewritten to provide a context for these global concepts, draw comparisons between terrestrial and aquatic systems, and introduce the concept of primary production.

We have increased representation of women and minority researchers in examples. Recognizing the importance of informing students of the diversity of scientists engaged in the sciences, previous editions have attempted to include contributions of women and minority researchers to the development of ecological science. That representation has been expanded in the eighth edition.

This edition increases the emphasis on the role of evolution in ecological science. Increasingly, evolutionary science informs and guides ecological research, not just within the field of evolutionary ecology. In response to reviewers' comments on this point, we have added examples and made additional connections between ecology and evolution in response to reviewer comments throughout the text. We have also expanded chapter 4 to include five new figures and several figure revisions to explain the relationships between genetic diversity, evolution, and ecological consequences, including an expansion of the treatment of non-Mendelian genetics.

The types of interactions among species have been expanded to include the full range recognized by ecologists. Chapter 13 now begins with a general discussion of how ecologists characterize species interactions. New examples are provided that explore amensalism and competition and the evolutionary and ecological consequences of these selective pressures. New figures have been created to illustrate these additions.

Coverage and connections to global-scale processes have been strengthened. Revisions of chapters 21 and 23 are aimed at providing greater clarity to the broad spectrum of global change phenomena. In addition, these revised chapters help connect coverage in preceding chapters of topics prominent in global change ecology.

The introductions and end-of-chapter review questions have been streamlined. In response to reviewer comments, we have trimmed the introductions to most chapters to move more quickly into the main content. Review questions have also been edited to make them more consistent in length and level of detail to encourage student engagement and to improve their clarity and accessibility.

The Investigating the Evidence boxes have been moved from the body of chapters to Appendix A at the end of the book. While we think that this series of exercises in study design and basic statistics remain a valuable adjunct to an introduction to ecology, many instructors have indicated that their presentation in the body of chapters interrupts the flow of the reading and distracts from the core content. By moving the evidence features to the end of the book, we have addressed these concerns, while making them available to instructors and students who find their content useful.

Significant Chapter-by-Chapter Changes

Chapter 1 An Applications discussion focused on how ecological science can inform environmental law and policy now concludes chapter 1. Citing the fact that, since ecological science concerns relationships between organisms and the environment, it is natural to turn to ecology when environmental concerns arise. This new feature addresses what is perhaps the most practical contribution that ecological science can make and provides a conceptual umbrella for Applications discussions in later chapters.

Chapter 2 The new introduction uses a desert ecology example to introduce the biome concept within the context of evolutionary pressure from both the physical and biological environments, in alignment with requests by reviewers. We now introduce the concept of primary production and the trophic cascade in this chapter to set the stage for in-depth treatment later. The global biomes are now presented with a new Whittaker diagram to explain the relationship between temperature, precipitation, and dominant vegetation. This is paired with, and corresponds to, the biomes as defined in previous editions, moving the figure of the world biomes from the back of the book to this chapter. In response to reviewer requests, we have also added a discussion and figures of the rain shadow effect and microclimates. The latter uses a new figure of the western United States to show the complexity of the biome concept at a finer geologic scale than is typically represented. Revisions have been made to the soil horizon figure to make it more representative and to the orbit of the earth figure to include the 0^{o} point.

Chapter 3 The introduction has been revised in response to reviewers' comments to directly compare terrestrial and aquatic systems, with a new table for students to consider particular physical features and their implications for the evolution of life in these distinctive environments. The structure of this chapter now better mirrors that of chapter 2. In response to reviewer requests, we have added a discussion and figure to explain thermohaline circulation and associated upwelling and their importance for aquatic life. Both the figure on streams and the one on lake turnover have been improved from the previous edition, with the latter revised to be simpler and more intuitive and show where fish primarily reside during different seasons. The figure on ocean currents now includes eight more seas, including Antarctic seas not shown in previous editions.

Chapter 4 In response to reviewer requests, the introduction now emphasizes why evolution belongs in an ecology textbook, and includes a new figure that shows how genetic diversity is expressed in phenotypic diversity and how this affects ecological interactions. We have included a new case study of research on crickets that illustrates the concepts of mutation, genetic drift, and natural selection, with corresponding figures. There is also a new figure to explain different mechanisms of genetic drift. Another new figure illustrates where alleles are in a population, and how this translates to quantifying allele frequencies and resulting investigation of deviations from Hardy-Weinberg equilibrium. Explanations of the latter and why it is important for ecology are made clearer. In response to reviewer requests, the figures on plasticity and on different types of selection have been revised to be easier to read. The discussion and explanation of quantitative genetics is strengthened in this edition. The relationships between evolution and ecological processes are strengthened throughout.

Chapter 13 The introduction has been rewritten to set the stage for the three chapters (13, 14, and 15) on species interactions and includes a summary table to explain the different classifications, based on impact to each organism. We have added explanations of both amensalism and commensalism, using new research examples, as well as describing how these categories overlap with other types of interactions such as competition. We also added an exciting, new research example for niche partitioning to replace the previous one on salt marsh grasses, illustrated by corresponding new figures.

Chapter 16 The community concept has been expanded to include a full range of interacting species, and presentation of the Shannon-Wiener index of species diversity has been edited to ease students into the mathematical expressions of the index. In addition, the discussion of the lognormal distribution has been updated to include recent analyses showing that it is one of several possible distributions of species abundance patterns. Finally, lower algal and plant diversity in response to nutrient enrichment is explained as a result of decreased environmental complexity, as competition for limiting nutrients and light is replaced by competition dominated by a single resource: light.

Chapter 20 Details of the successional sequence at Glacier Bay, Alaska, have been trimmed to make room for a broader historical perspective on ecological succession by introducing the views of two major contributors to the subject, Frederic E. Clements and Henry A. Gleason. Introducing the ideas of these pioneering researchers provides a basis for a more refined perspective on the process of succession and the nature of "climax" communities. The chronosequence at Glacier has been visualized by a series of photos of key points along the sequence. In addition, the concept of a chronosequence is introduced early in the chapter and a contrast is made between the use of chronosequences versus direct observations to study successional change.

Chapter 21 The new Applications feature, which concerns using landscape approaches to mitigating urban heat islands, is intended to focus landscape ecology on the environment where most people, including students, now live. This new feature also connects the landscape ecology chapter to earlier discussions of urban ecology as a research frontier (chapter 1), urban heat islands (chapter 5), biodiversity in urban landscapes (chapter 16), and nutrient fluxes across the urban landscape (chapter 19). This discussion also foreshadows a detailed review of global climate warming in chapter 23.

Chapter 23 In response to reviewers' comments, we have revised the introduction to emphasize the multidisciplinary nature of global ecology and that there are many components of global change in addition to climate. Connections between previous chapters and these fields have also been strengthened. A research example that reflects the more recent explorations into the ecological importance of La Niña events has been added with a corresponding figure. Figure revisions incorporate more current data that emphasize the connections between carbon and temperature increases, including both the modern-age relationships with anthropogenic carbon and patterns at the millennial scale.

Online Materials

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

Design elements: (bat and cactus flower): ©Johner Images/Getty Images

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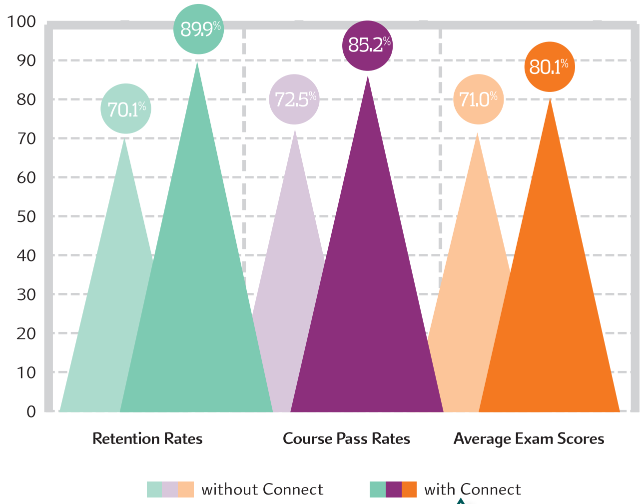

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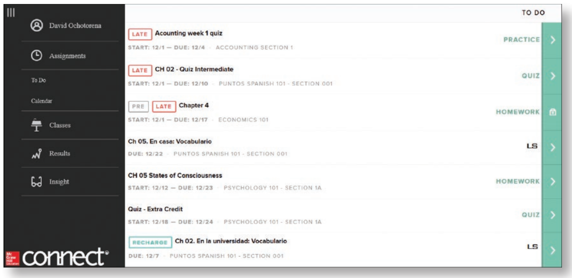

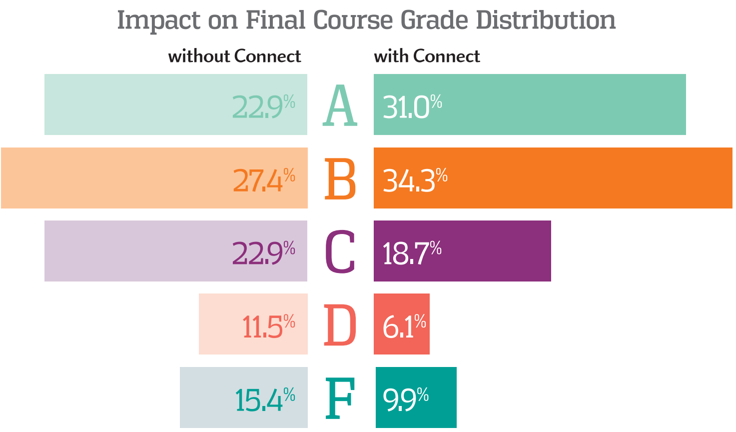

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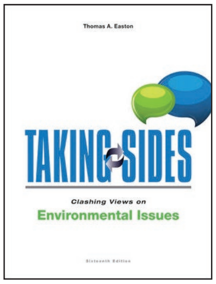

Taking Sides: Clashing Views on Environmental Issues,
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Taking Sides presents current controversial issues in a debate-style format designed to stimulate student interest and develop critical thinking skills. Each issue is thoughtfully framed with an issue summary, an issue introduction, and a postscript or challenge questions. An online Instructor's Resource Guide with testing material is available. Available through Create.

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

A complete list of the people who have helped us with this project would be impossibly long. However, during the development of this textbook, many colleagues freely shared their ideas and expertise, reviewed new sections, or offered the encouragement a project like this needs to keep it going: Roger Arditi, Art Benke, Scott Collins, Cliff Dahm, Arturo Elosegi, Lev Ginzburg, Manuel Graça, Tom Kennedy, Tim Lowrey, Sam Loker, Rob Miller, Will Pockman, Steve Poe, Bob Sinsabaugh, Alain Thomas, Tom Turner, John Vucetich, Leah Vucetich, Lawrence Walker, Chris Witt, Blair Wolf.

We would like to especially thank Shannon Murphy and Robin Tinghitella for their extensive suggestions for the eighth 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 during this project, including Justin Wyatt, Elizabeth Sievers, Kelly Brown, Susan Trentacosti, David Hash, and Melissa Homer.

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 eighth edition. Their depth and breadth of knowledge and experience, both as researchers and teachers, are humbling. They continue our education, for which we are grateful, and we honestly could not have continued the improvement of this textbook without them.

Finally, we wish to thank our families for support and encouragement given throughout the production of the eighth edition.

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Chapter 1

Introduction to Ecology

Historical Foundations and Developing Frontiers

Source: Jeff Foot/NPS

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 may 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, which is at the base of figure 1.1, 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 individuals of a single species inhabiting a defined area. 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.

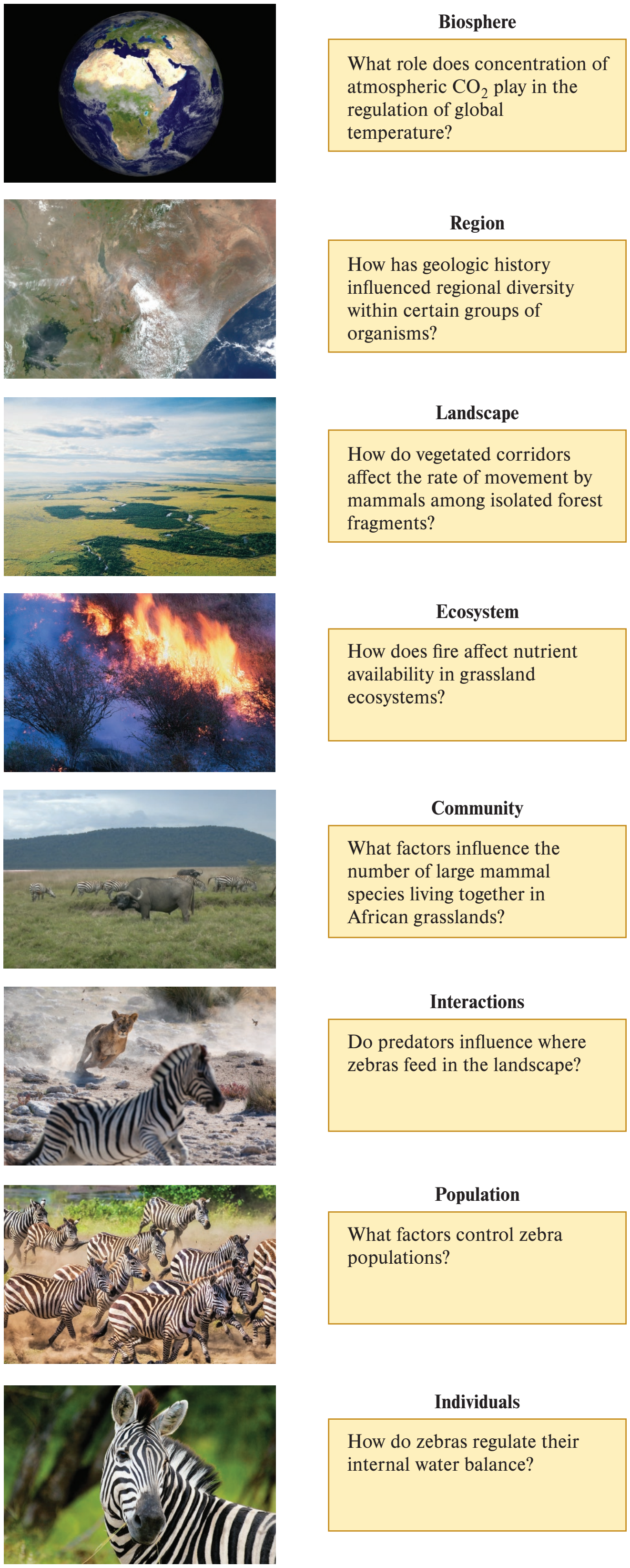


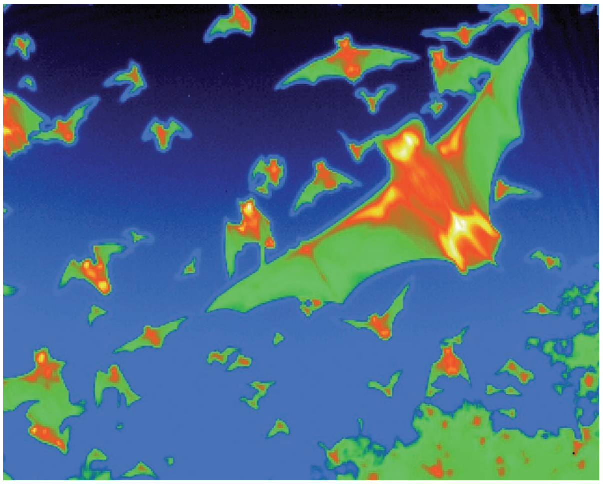
Figure 1.1 Levels of ecological organization and examples of the kinds of questions asked by ecologists working at each level. These ecological levels correspond broadly to the sections of this book. ©Calysta Images/Getty Images RF; Source: NASA-Goddard Space Flight Center; ©Comstock/PunchStock RF; Source: Gary Wilson/USDA Natural Resources Conservation Service; ©Anna Sher; ©Mogens Trolle/Shutterstock RF; ©cinoby/Getty Images RF; ©Glow Images RF

Bringing biological components of the environment into the picture takes us to the next level of organization, the ecology of interactions such as predation, parasitism, and competition. 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 definition of an ecological community as an association of interacting species links community ecology with the ecology of interactions. 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.

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. However, landscapes are not isolated either but part of geographic regions subject to large-scale and long-term regional processes. These regional processes are the subjects of geographic ecology. Geographic 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.

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).



(a)

(b)

Figure 1.2 Two rapidly developing frontiers in ecology. (*a*) **Aeroecology:** the interdisciplinary study of the ecology of the earth–atmosphere boundary (Kunz et al. 2008). New tools, such as the Indigo/FLIR Merlin midthermal camera that took this thermal infrared image of flying Brazilian free-tailed bats, *Tadarida brasiliensis,* have opened this developing frontier in ecology. This image depicts variation in the surface temperature of these bats. Thermal infrared technology makes it possible not only to detect and record the presence of free-ranging nocturnal organisms, but also to investigate their physiology and ecology in a noninvasive manner (see chapter 5). (*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*) ©Nickolay I. Hristov and Thomas H. Kunz; (*b*) ©Jon Bilous/Shutterstock RF

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 be relevant, for example, does an ecologist studying factors limiting numbers in a population of zebras need to consider the influences of interactions with other species or the influences of food on the survival of individuals?

1.2 Sampling Ecological Research

LEARNING OUTCOMES

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

1.5 Describe some emerging frontiers in ecology.
1.6 Explain how the use of stable isotopes has extended what it is possible to know about the ecology of warblers.
1.7 Compare the spatial and temporal scales addressed by the research of Robert MacArthur, Nalini Nadkarni, and Margaret Davis.

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.

The Ecology of Forest Birds: Old Tools and New

Robert MacArthur gazed intently through his binoculars. He was watching a small bird, called a warbler, searching for insects in the top of a spruce tree. To the casual observer it might have seemed that MacArthur was a weekend bird-watcher. Yes, he was intensely interested in the birds he was watching, but he was just as interested in testing ecological theory.

The year was 1955, and MacArthur was studying the ecology of five species of warblers that live together in the spruce forests of northeastern North America. All five warbler species, Cape May (*Dendroica tigrina*), yellow-rumped (*D. coronata*), black-throated green (*D. virens*), blackburnian (*D. fusca*), and bay-breasted (*D. castanea*), are about the same size and shape and all feed on insects. Theory predicted that two species with identical ecological requirements would compete with each other and that, as a consequence, they could 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.

The warblers fed mainly by gleaning insects from the bark and foliage of trees. MacArthur predicted that these warblers might be able to coexist and not compete with each other if they fed on the insects living in different zones within trees. To map where the warblers fed, he subdivided trees into vertical and horizontal zones. He then carefully recorded the amount of time warblers spent feeding in each.

MacArthur's prediction proved to be correct. His quantitative observations demonstrated that the five warbler species in his study area fed in different zones in spruce trees. As figure 1.3 shows, the Cape May warbler fed mainly among new needles and buds at the tops of trees. The feeding zone of the blackburnian warbler overlapped broadly with that of the Cape May warbler but extended farther down the tree. The black-throated green warbler fed toward the trees' interiors. The bay-breasted warbler concentrated its feeding in the middle sections of trees. Finally, the yellow-rumped warbler fed mostly on the ground and low in the trees. MacArthur's observations showed that though these warblers live in the same forest, they extract food from different parts of that forest. He concluded that feeding in different zones may reduce competition among the warblers of spruce forests.

MacArthur's study (1958) of foraging by warblers is a true classic in the history of ecology. However, like most studies it raised as many questions as it answered. Scientific research is important both for what it teaches us directly about nature and for how it stimulates other studies that improve our understanding. MacArthur's work stimulated numerous studies of competition among many groups of organisms, including warblers. Some of these studies produced results that supported his work and others produced different results. All added to our knowledge of competition between species and of warbler ecology.

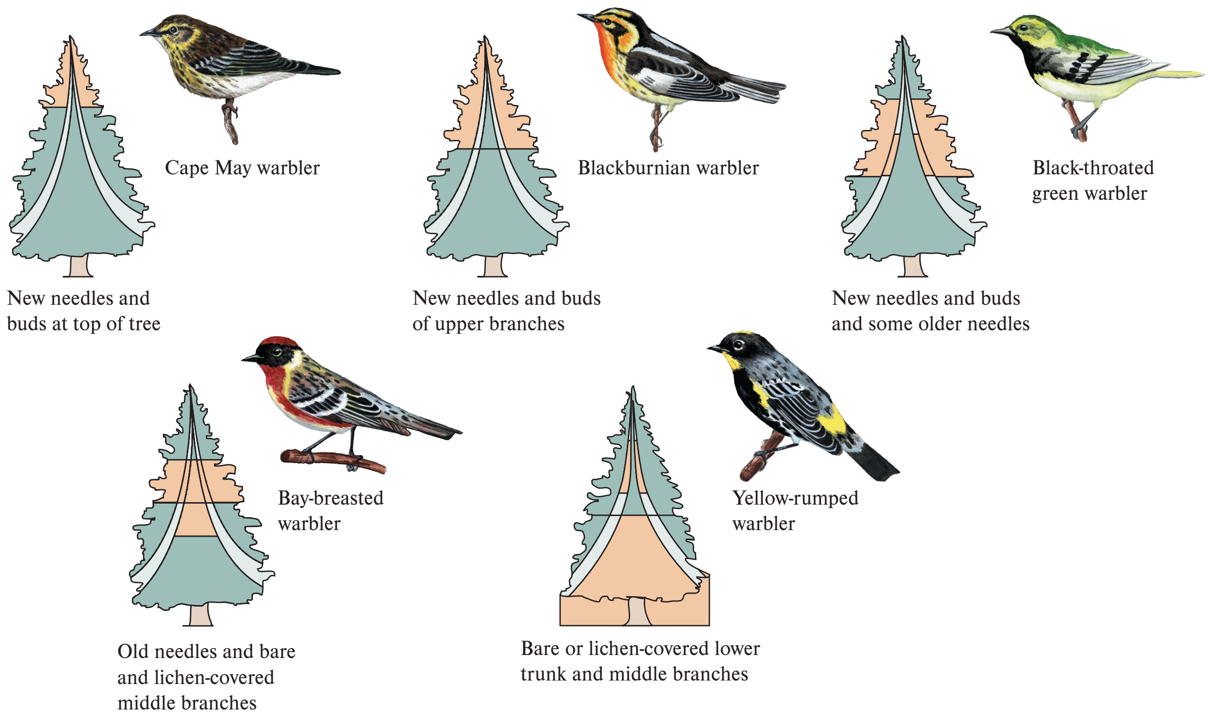


Figure 1.3 Warbler feeding zones shown in beige. The several warbler species that coexist in the forests of northeastern North America feed in distinctive zones within forest trees.

Figure 1.4 A male American redstart, *Setophaga ruticilla.* Mature male American redstarts are highly territorial, dominating high-quality feeding territories in their tropical wintering grounds, pushing most female redstarts and young males into poorer-quality feeding habitats.
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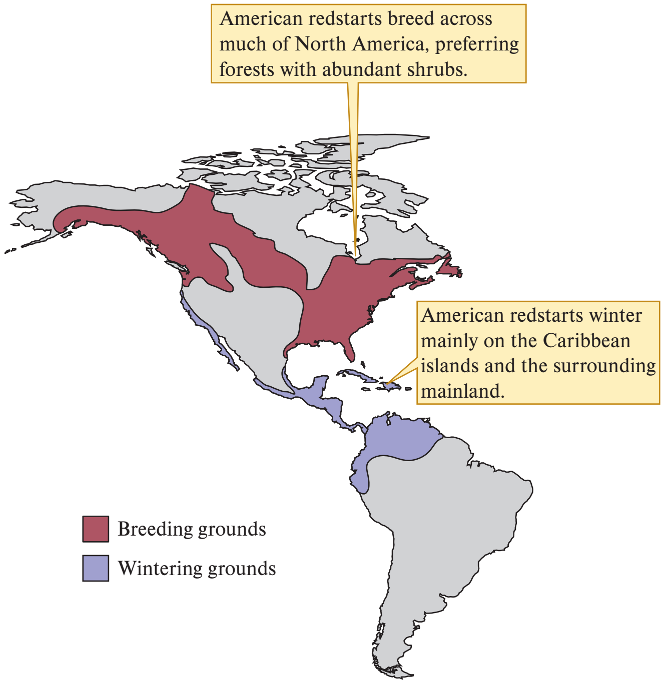

Figure 1.5 Map of the breeding and wintering grounds of the American redstart, *Setophaga ruticilla.*

Nearly half a century after Robert MacArthur studied the feeding ecology of warblers through the lenses of his binoculars, a team of Canadian and U.S. scientists led by Ryan Norris (Norris et al. 2005) worked to develop tools capable of penetrating the feeding habitats of wide-ranging migratory birds. The object of their study was the American redstart (*Setophaga ruticilla*), another colorful member of the warbler family Parulidae (fig. 1.4). American redstarts, like the warblers studied by MacArthur, are long-distance migrants, nesting in temperate North America but spending their winters mainly in tropical Central America, northern South America, and the Caribbean islands.

Historically, studies of wide-ranging bird species, such as the American redstart, have focused mainly on their temperate breeding grounds. However, observations by ecologists had long suggested that the success of an individual migratory bird during the breeding season may depend critically on the environmental conditions it experienced on its tropical wintering grounds. For example, it has been well established that male migratory birds, arriving early on the breeding grounds, are generally in better physical condition compared to those arriving later. Early arrivals also generally obtain the best breeding territories and have higher reproductive success.

Variation in arrival times and physical condition led ecologists to ponder the connection between events on the wintering grounds and subsequent reproductive success among birds in their breeding habitats. To answer such a question, we need a great deal of information, including where individual birds live on the wintering grounds, how the winter habitat correlates with physical condition during migration, how winter habitat influences time of arrival on the breeding grounds, and whether winter habitat correlates with reproductive success on the breeding grounds. Clearly, the amount of information required to answer such questions, concerning environments separated by thousands of kilometers (fig. 1.5), exceeds what one person, or even a large team, can learn through the lenses of binoculars.

Often, ecologists have pioneered the use of more powerful research tools, as the complexity of their questions have increased. A tool to which ecologists turn increasingly to understand the ecology of migratory birds is **stable isotope analysis** (see chapter 6). Isotopes of a chemical element, for example, isotopes of carbon, have different atomic masses as a result of having different numbers of neutrons. Carbon, for instance, has three isotopes (listed in order of increasing mass): ^{12}C, ^{13}C, and ^{14}C. Of these three, ^{12}C and ^{13}C are stable isotopes because they do not undergo radioactive decay, whereas ^{14}C decays radioactively and is therefore unstable. Stable isotopes have proven useful in the study of ecological processes—for example, identifying food sources, because the proportions of various isotopes differ across the environment.

Stable isotope analysis provides ecologists with a new type of "lens" capable of revealing ecological relationships that would otherwise remain invisible. For example, ecologists using stable isotope analysis can track habitat use by American redstarts on their wintering grounds. In Jamaica, older male American redstarts, along with some females, spend the winter in higher-productivity mangrove forest habitats, pushing most females and younger males into poorer-quality, dry scrub habitat. The dominant plants in these two habitats and the insects that feed on them contain different proportions of the carbon isotopes ^{12}C and ^{13}C. Therefore, the tissues of the birds spending their winters in the productive mangrove habitat (lower ^{13}C) and those spending the winters in the poor scrub habitat (higher ^{13}C) are in effect chemically tagged. As a consequence, today's ecologist can analyze a very small sample of blood from an American redstart when it arrives on its temperate breeding ground and know the habitat where it spent the winter. When Ryan Norris and his research team made such measurements, they found that male redstarts that had spent the winter in the more productive mangrove habitat arrived on the breeding grounds earlier and produced significantly more young birds that survived to fledging.

Stable isotope analysis and the role that it has played in elucidating the ecology of a diversity of organisms will thread its way through the text. As is often the case in science, new tools create new research frontiers. Another of those frontiers is to be found in the canopies of forests.

Forest Canopy Research: A Physical and Scientific Frontier

Studies of warblers showcase how ecologists approach studies of one or a few species. Other ecologists have been concerned with the ecology of entire forests, lakes, or grasslands, which they treat as ecosystems. An **ecosystem** includes all the organisms that live in an area and the physical environment with which those organisms interact. Many ecosystem studies have focused on **nutrients,** the raw materials that an organism must acquire from the environment to live.

For ecologists who study the budgets of nutrients such as nitrogen, phosphorus, or calcium, one of the first steps is to inventory their distribution within an ecosystem. Inventories by Nalini Nadkarni (1981, 1984a, 1984b) changed our ideas of how tropical and temperate rain forests are structured and how they function. On the rain forest floor, she had wondered about the diversity of organisms and ecological relationships that might be hidden in the canopy high above. Her wonder soon gave way to determination. With the aid of mountain-climbing equipment, Nadkarni slowly made her first ascent into the canopy of the Costa Rican rain forest, a world explored by few others and where she was to become a pioneer (fig. 1.6). Nadkarni not only visited the canopy but also was among the first to explore the ecology of this unseen world.

Because of leaching by heavy rains, many rain forest soils are poor in nutrients such as nitrogen and phosphorus. The low availability of nutrients in many rain forest soils has produced one of ecology's puzzles. How can the prodigious life of rain forests be maintained on such nutrient-poor soils? Many factors contribute to the maintenance of this intense biological activity. Nadkarni's research in the treetops uncovered one of those factors, a significant store of nutrients in the rain forest canopy.

The nutrient stores in the rain forest canopy are associated with epiphytes. **Epiphytes** are plants, such as many orchids and ferns, that live on the branches and trunks of other plants. Epiphytes are not parasitic: they do not derive their nutrition from the plant they grow on. As they grow on the branches of a tree they begin to trap organic matter, which eventually forms a mat. Epiphyte mats increase in thickness up to 30 cm, providing a complex structure that supports a diverse community of plants and animals.

Figure 1.6 Exploring the rain forest canopy. What Nalini Nadkarni discovered helped solve an ecological puzzle. Courtesy Nalini Nadkarni, photo by Dennis Paulson

Epiphyte mats contain significant quantities of nutrients. Nadkarni estimated that these quantities in some tropical rain forests are equal to about half the nutrient content of the foliage of the canopy trees. In the temperate rain forests of the Olympic Peninsula in Washington, the mass of epiphytes is four times the mass of leaves on their host trees.

Nadkarni's research showed that in both temperate and tropical rain forests, trees access these nutrient stores by sending out roots from their trunks and branches high above the ground. These roots grow into the epiphyte mats and extract nutrients from them. As a consequence of this research, we now know that to understand the nutrient economy of rain forests the ecologist must venture into the treetops.

Easier means of working in the rain forest canopy have been developed, and this research is no longer limited to the adventurous and agile. New ways to access the forest canopy range from hot air balloons and large cranes (see Investigating the Evidence 16 in Appendix A) to aerial drones (fig. 1.7). Research projects supported—and made far easier—by these technologies have included the ecology of migratory birds in the forest canopy, photosynthesis by epiphytes living at different canopy heights, and vertical stratification of habitat use by bats and beetles (Ozanne et

Figure 1.7 Aerial drones now provide a powerful tool for monitoring a wide range of ecosystems and wild populations. ©Halfpoint/Shutterstock RF

al. 2003). Nadkarni points out, in response to these developments, that the canopy as a physical frontier may be closing, but its exploration as a scientific frontier is just beginning, particularly as we attempt to predict the ecological consequences of climate change.

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 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 1.8, 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. William Bradshaw and Christina Holzapfel (2006) summarized several studies documenting evolutionary change in northern animals, ranging from birds and insects to small mammals (fig. 1.9), in response to longer growing seasons with global warming (see chapter 23). Such research will be essential to predicting ecological responses to global climate change.

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 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.

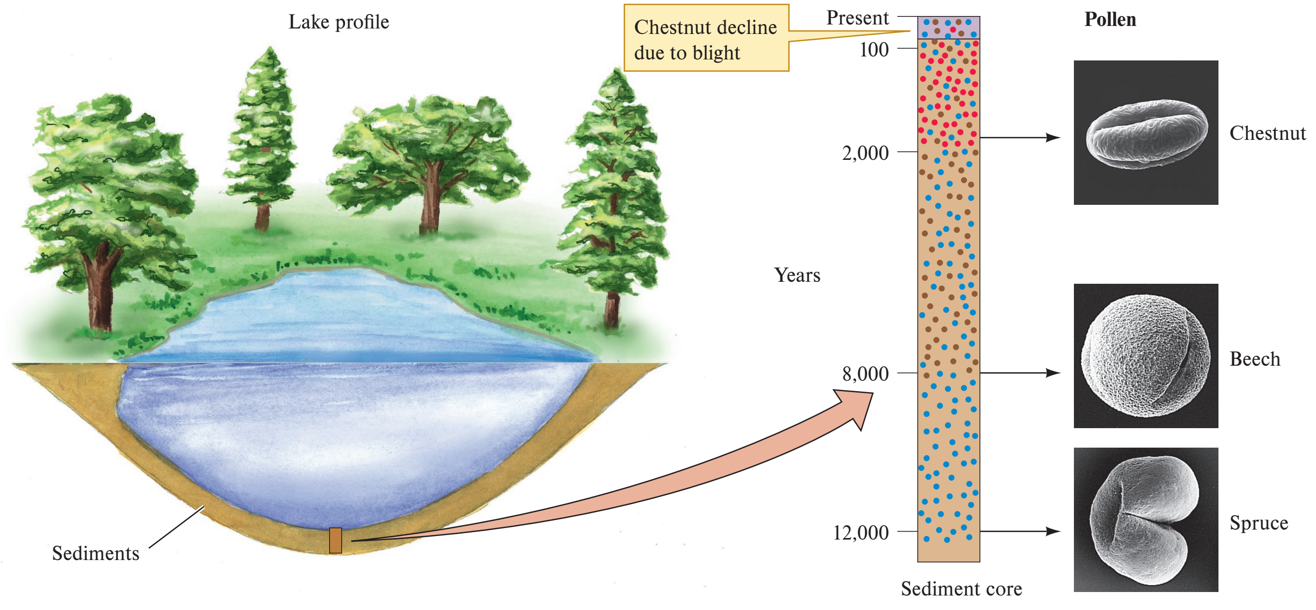

Figure 1.8 The vegetation history of landscapes can be reconstructed using the pollen contained within the sediments of nearby lakes. (*all photos*): Courtesy of the Gretchen and Stanley Jones Palynological Collection and the Botanical Research Institute of Texas

Figure 1.9 Studies indicate that North American red squirrels, *Tamiasciurus hudsonicus,* have been undergoing rapid evolution for earlier breeding, during a recent period of increased average spring temperatures in Canada's Yukon Territory (Réale et al. 2003). ©Paul Reeves Photography/Shutterstock RF

Concept 1.2 Review

1. How were the warbler studies of Robert MacArthur and those that focused on the American redstart similar? How did they differ?
2. What aspects of Nalini Nadkarni's research identify it as "ecosystem ecology"? Give examples of research in forest canopies that would address other levels of ecological organization (for examples, see fig. 1.1).
3. The discussion of the research by Margaret Davis and her colleagues did not identify the questions that they addressed. What research questions can we infer from the above description of their work?

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, which includes how the environment influences the distribution and abundance of species (covered in chapters 9–12), 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 International Trade in Endangered Species of Wild Fauna and Flora (CITES), an international treaty to protect endangered species from the threat of wildlife trafficking and trade. The second was the U.S. Endangered Species Act, or ESA.

The ESA extended protection to all threatened and endangered vertebrate animals, invertebrate animals, and plants in the United States and to species elsewhere around the globe listed as endangered under the CITES treaty. The species protected by the ESA have ranged from the large and charismatic, such as grizzly bears and whales, to inconspicuous plants and insects. Later amendments to the ESA required that management agencies, such as the U.S. Fish and Wildlife Service, identify "critical habitat" for threatened and endangered species. This requirement brought studies of the adaptations of species to the environment (chapters 4–8) as well as community, ecosystem, landscape, and geographic ecology (chapters 16–22), into greater prominence as tools for endangered species management. Because human-caused changes to the environment now extend to the entire planet, global ecology (chapter 23) is increasingly relevant to long-term endangered species protection.

Ecological studies are also essential to determining whether protected populations have recovered sufficiently to be removed from the ESA's list of endangered species, a process called *delisting*. There have been a number of high-profile species that have been delisted in recent years, including the gray whales of the eastern North Pacific Ocean and bald eagles of the contiguous 48 states. In summary, ecological science has been essential to identifying, protecting, and managing species vulnerable to extinction.

Summary

Ecologists study environmental relationships ranging from those of individual organisms to factors influencing global-scale processes. The research focus and questions posed by ecologists differ across the levels of ecological organization studied.

Ecologists design their studies based on their research questions, the temporal and spatial scale of their studies, and available research tools. With this brief review of research approaches and topics, we return to the question asked at the beginning of the chapter: What is ecology? Ecology is indeed the study of relationships between organisms and the environment. However, as you can see from the studies reviewed, ecologists study those relationships over a large range of temporal and spatial scales using a wide variety of approaches. Ecology includes Davis's studies of vegetation moving across the North American continent over a span of thousands of years. Ecology also includes the observational studies of birds in contemporary forests by MacArthur. Ecologists may study processes on plots measured in square centimeters or, like those studying the ecology of migratory birds, study areas may span thousands of kilometers. Important ecological discoveries have come from Nadkarni's probing of the rain forest canopy and from traces of stable isotopes in a droplet of blood. Ecology includes all these approaches and many more. Because ecological science concerns relationships between organisms and the environment, it is often consulted when environmental concerns arise. Ecological science has been particularly important to identifying, protecting, and managing species vulnerable to extinction.