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.

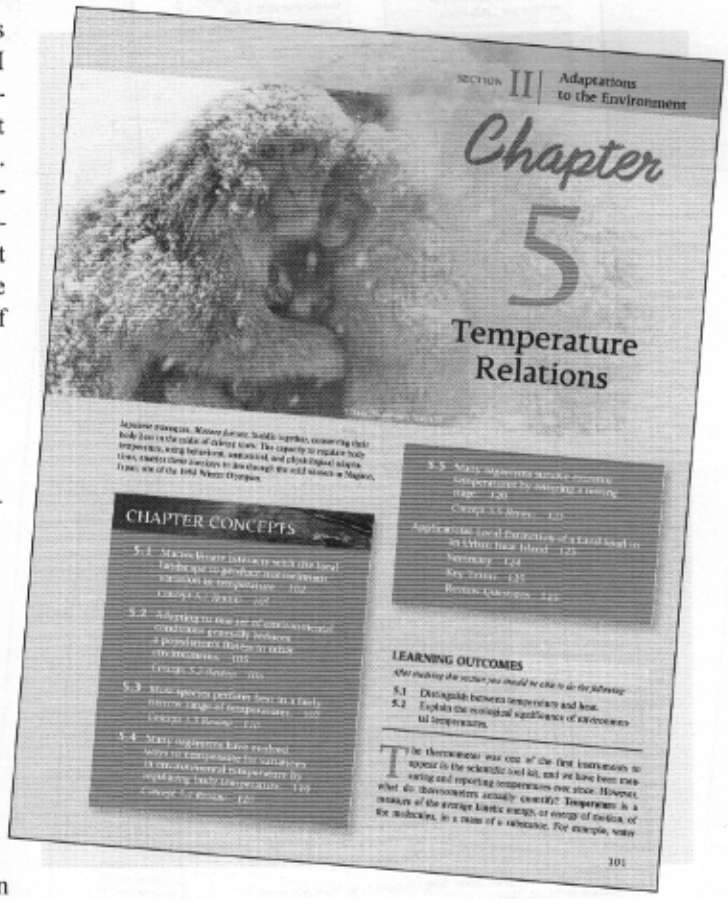
Features Designed with the Student in Mind

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

CHAPTER CONCEPTS

LEARNING OUTCOMES

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.

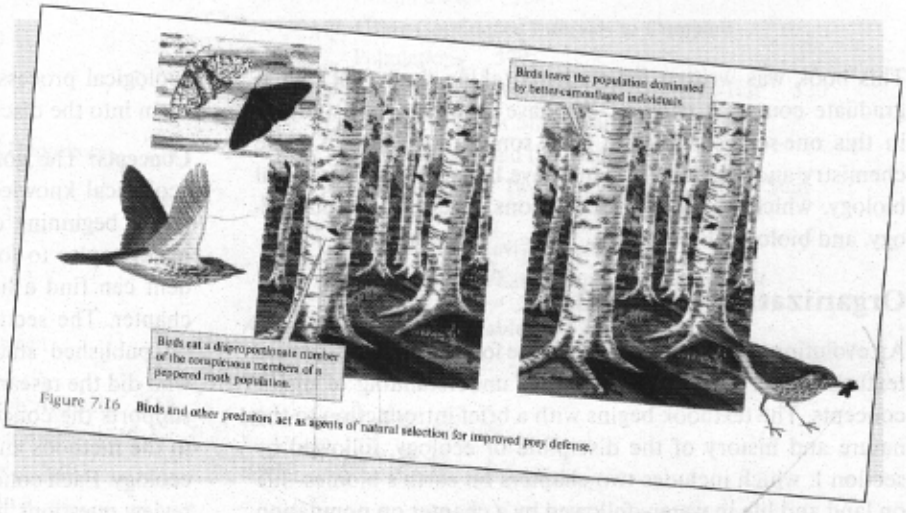


Figure 7.16 Birds and other predators act as agents of natural selection for improved prey defense.

Visualizing a process involving a predator and its prey.

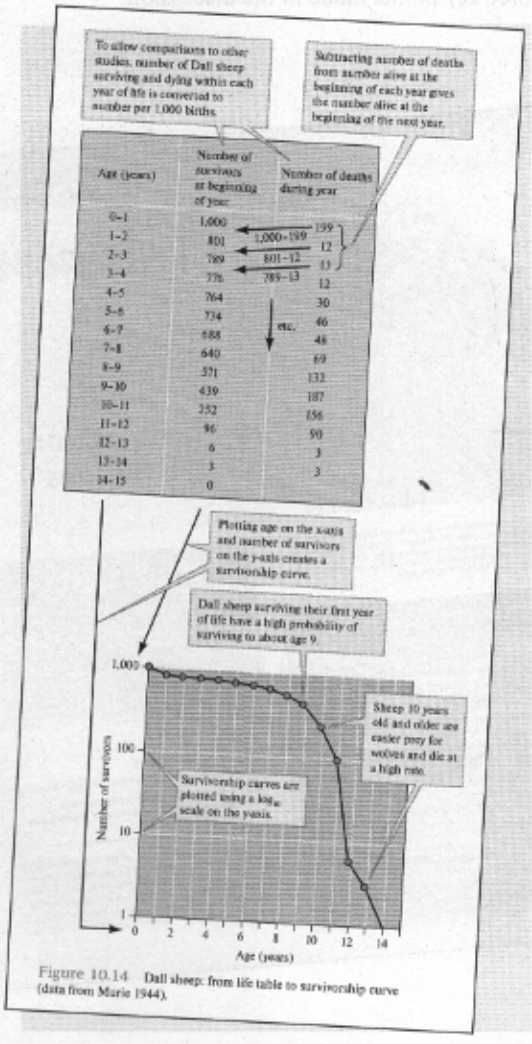


Figure 10.14 Dall sheep: from life table to survivorship curve (data from Murie 1944).

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

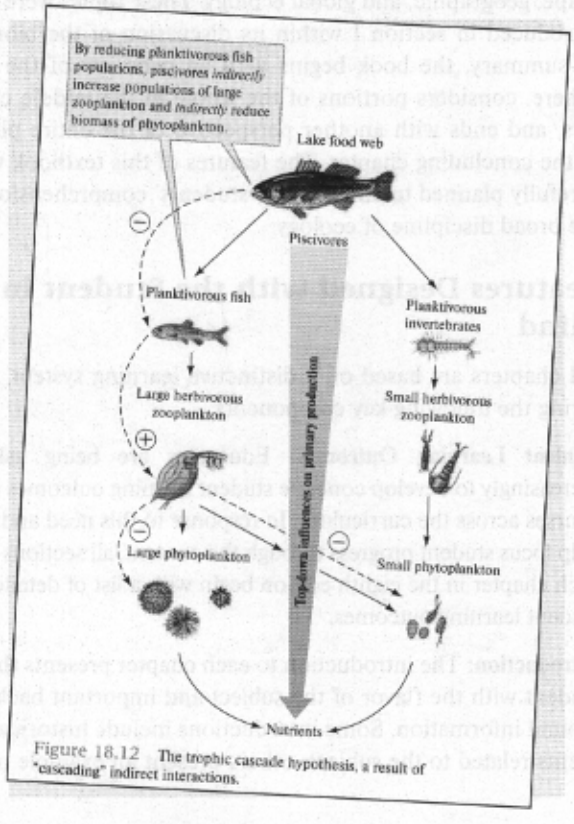


Figure 18.12 The trophic cascade hypothesis, a result of "cascading" indirect interactions.

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.
- ***Index***


520 Appendix A Investigating the Evidence

✓ Information
Hypothesis
Predictions
Testing

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 classifying critical habitat for rare or threatened species. However, determining the number of species in a community is not a simple undertaking. Several 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 a real sensing 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 30 fire-out 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 subclasses 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 leaf nematodes. They sampled these taxa from 1992 to 1994 and spent several years just sorting and cataloging the approximately 2,000 species collected. This work required approximately 10,000 scientific 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 ecological diversity of just 1 hectare of tropical forest would require from 300,000 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 in 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: 35,679 in dry forest versus 30,352 in rain forest. However, his collections in rain forest included 37% more beetle species than in dry forest: 1,063 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:

9.35 List the seven forms of rarity described by Rabinowitz.

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

9.37 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 the time of rapid climatic 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 textures, 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 (but not 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 are associated with the pristine ecosystems, *Colonia formosissima*, 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 size of ecologists by Jha 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, plankton, insects, scale insects, bivalves, butterflies, 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 position 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 rare attribute of rarity was not enough to make the peregrine vulnerable to extinction. The fatal setback finding 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 regulations 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 Sumatran 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° 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.