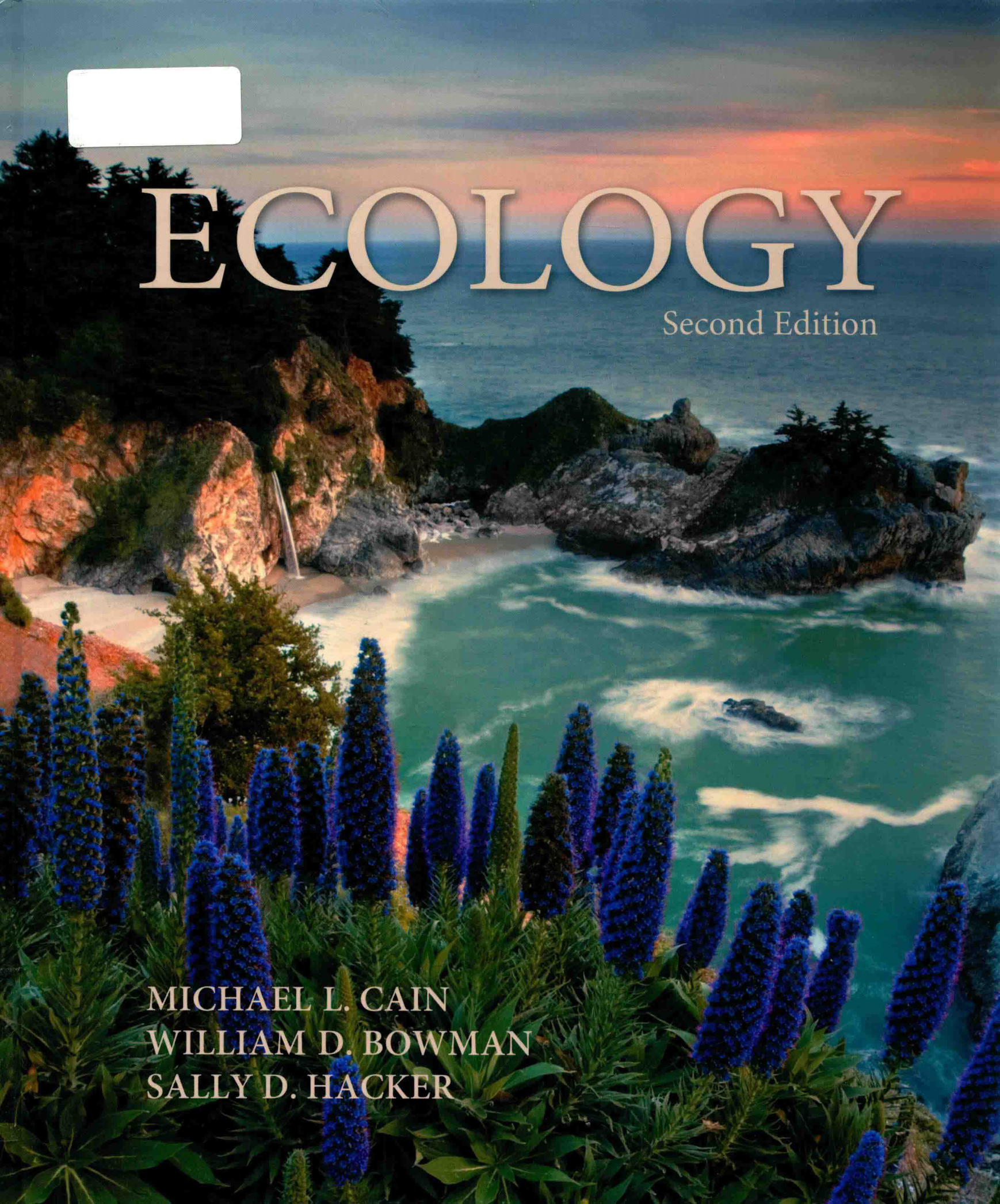
ECOLOGY
Second Edition
MICHAEL L. CAIN
WILLIAM D. BOWMAN
SALLY D. HACKER

ECOLOGY

Second Edition

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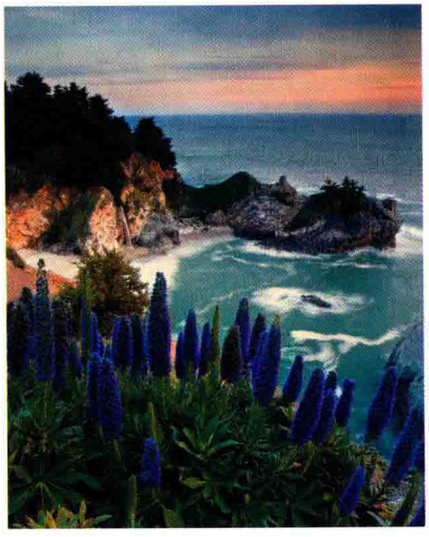

Cover photograph

Pride of Madeira (*Echium candicans*) blooms in Julia Pfeiffer Burns State Park, California. Photo © Tomas Kaspar/Alamy.

Ecology, Second Edition

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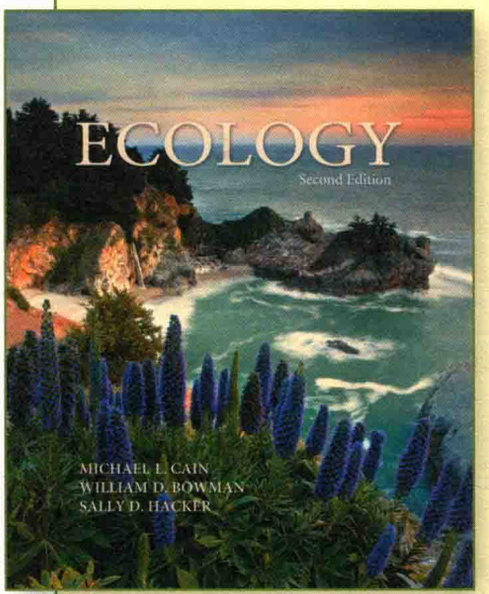
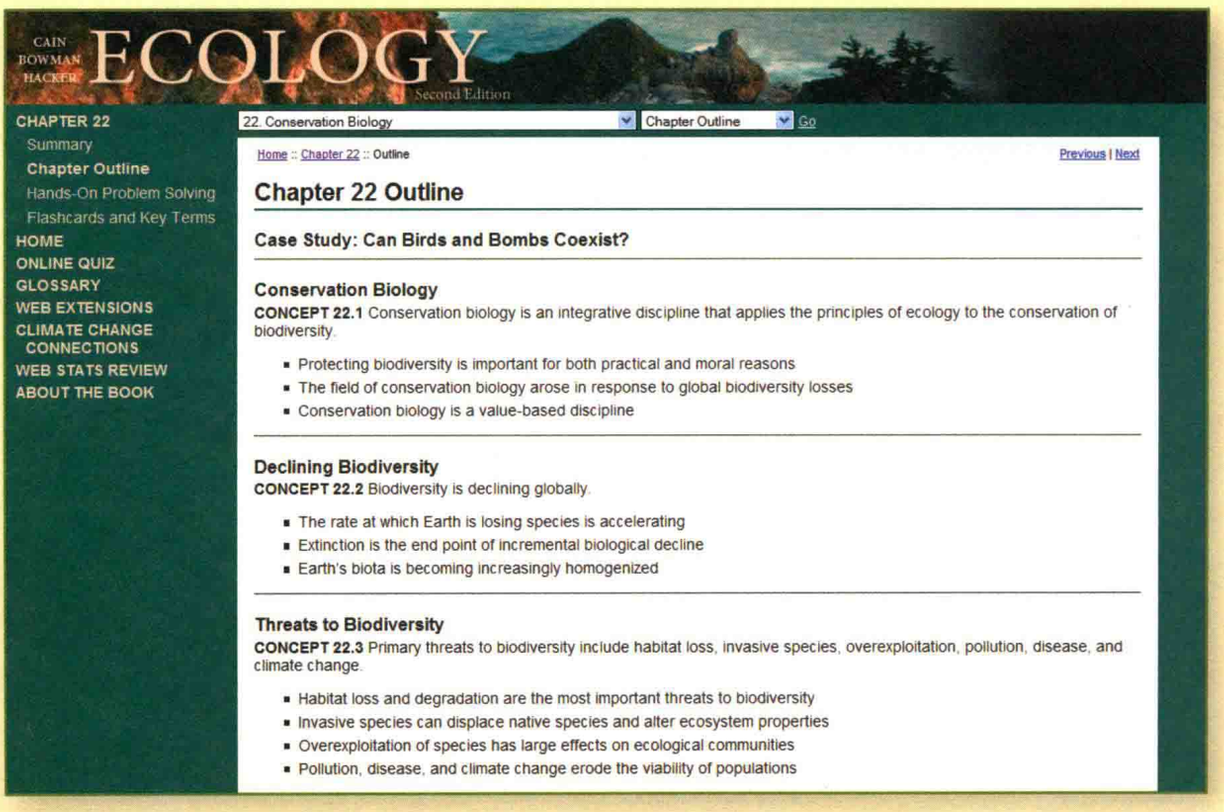
ECOLOGY SECOND EDITION

Companion Website

sites.sinauer.com/ecology2e

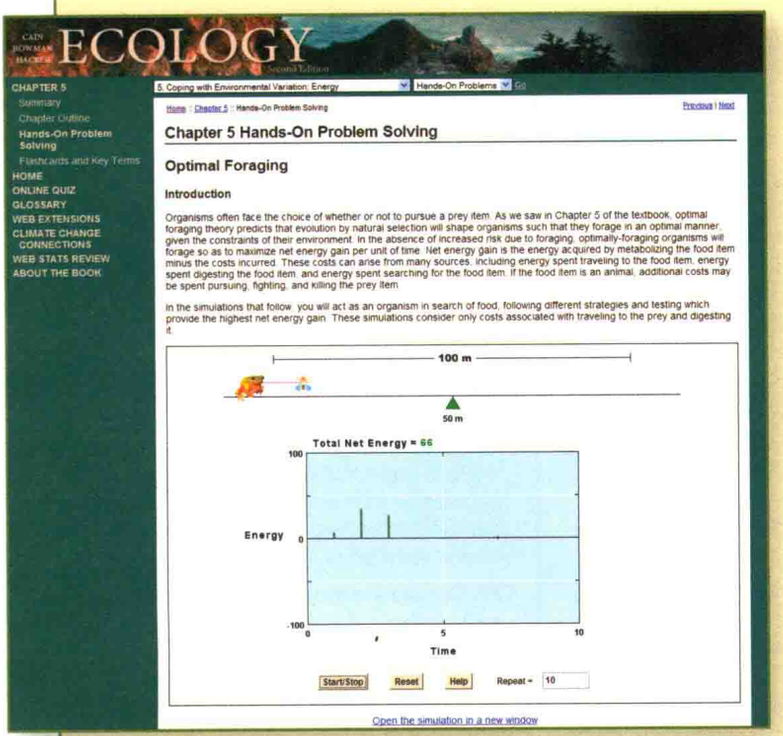


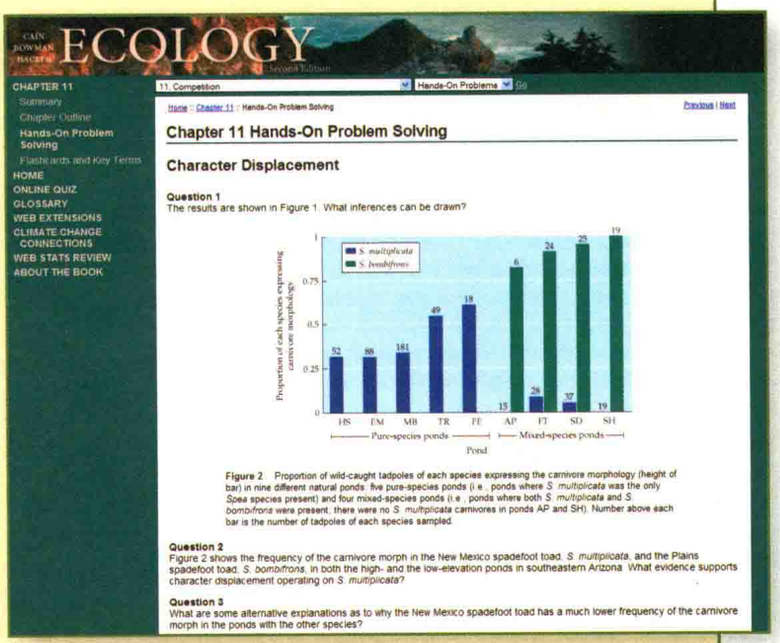
The **ECOLOGY** website is a valuable companion to the textbook that can help you learn and review the material introduced in your ecology course. Available free of charge, the site is designed to help you learn the concepts and terminology introduced in each chapter, as well as apply them to real-world problems. The site includes material that expands on the textbook's coverage of selected topics, resources to help you review each chapter, self-study tools for learning the terminology and checking your comprehension of key concepts and facts, and hands-on problems that involve you in working with data from actual experiments and simulations of model systems.



Features of the Companion Website

Hands-On Problem Solving Exercises: These inquiry-based exercises challenge you to think as a scientist and to analyze and interpret experimental data. Exercises include data manipulation questions based on real experiments, as well as problems involving simulations of model systems.





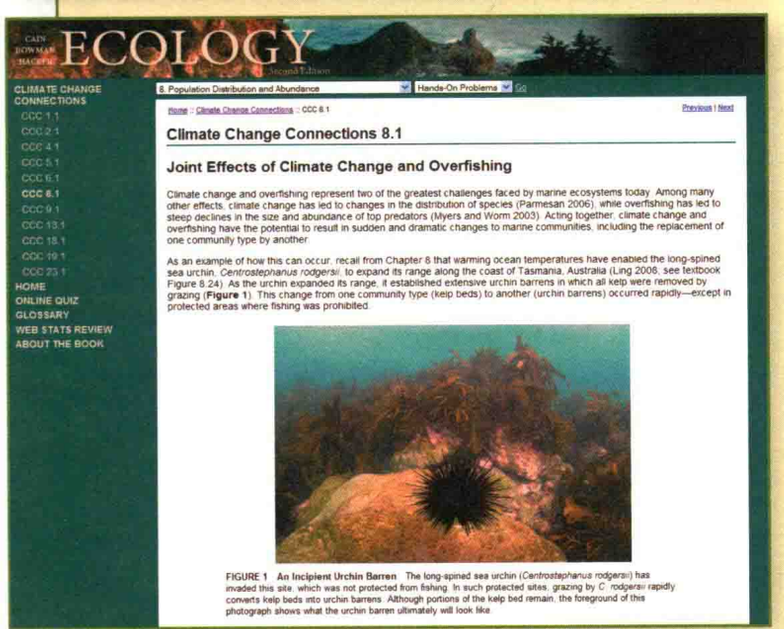


FIGURE 1 **An Incipient Urchin Barren** The long-spined sea urchin (*Centrostephanus rodgersii*) has invaded this site, which was not protected from fishing. In such protected sites, grazing by *C. rodgersii* rapidly converts kelp beds into urchin barrens. Although portions of the kelp bed remain, the foreground of this photograph shows what the urchin barren ultimately will look like.

Climate Change Connections: Referenced at specific points in the textbook, the Climate Change Connections relate topics introduced in the textbook to other levels of the ecological hierarchy, and help you better understand ongoing climate change.

ADDITIONAL FEATURES OF THE Companion Website:

- **Online Quizzes:** Multiple-choice quizzes cover all the main topics presented in each chapter. Your instructor may assign these quizzes, or they may be made available to you as self-study tools. (Instructor registration is required for student access to the quizzes.)
- **Chapter Outlines and Summaries:** Concise overviews of the important concepts and topics covered in each chapter.
- **Flashcards & Key Terms:** Flashcard activities help you master the many new terms introduced in each chapter of the textbook.
- **Web Extensions:** Expanded and additional coverage of selected topics introduced in the textbook.
- **Web Stats Review:** A brief review of statistical methods and techniques mentioned in the textbook.
- **Glossary:** A complete online version of the glossary, for quick access to definitions of important terms.
- **Suggested Readings** for each chapter of the textbook.

Hands-On Problem Solving Exercises

The following Hands-On Problems are available on the Companion Website (sites.sinauer.com/ecology2e).

1. Mosquitoes, Drought, and Disease: This Web exercise explores the connections between mosquito populations, periodic drought, and the incidence of mosquito transmitted diseases. You will read a recent paper that shows that mosquito populations increase in size after droughts. You will then plot data on drought severity compared to incidence of disease, and discuss implications for human health.

2. Simulating Seasons: This Web exercise illustrates connections between the axial tilt of Earth and temperature variation. Seasonal patterns and the range of temperature variations result from the degree of axial tilt. You will use a simulation model of Earth to vary axial tilt and explore latitudinal and seasonal variations in temperature.

3. Changing Climate and Changing Tree Lines: This Web exercise explores connections between elevation of tree lines and climate patterns. You will read a paper that discusses factors determining upper tree lines and which types of tree lines are likely to advance with changes in temperature. You will then plot recent temperature changes in high elevation areas and discuss the probability of tree line advance there.

4. Thermal Adaptations in Urban Ants: This Web exercise demonstrates thermal adaptations in ants that live in cities. You will investigate whether adaptations to heat in urban leaf-cutter ants reduces tolerance to cold temperatures.

5. Optimal Foraging: This Web exercise illustrates patterns of movement predicted by optimal foraging. Foraging decisions are based on relative costs and benefits. You will manipulate the foraging decision rules of a predator to explore how distance to and size of prey influence foraging strategies and benefits.

6. Effects of Natural Selection and Genetic Drift: This Web exercise demonstrates how natural selection and genetic drift can alter the frequencies of alleles in populations. You will investigate the effects of manipulating population sizes (and thus the strength of genetic drift) and strengths of selection.

7. The Growth/Reproduction Trade-off: This Web exercise explores the trade-off that species must make between growth and reproduction. You will investigate the effects of manipulating the set point at which fish start allocating resources into reproduction rather than further growth, under different levels of predation.

8. Effort and Accuracy of Population Estimates: This Web exercise illustrates the relationship between the effort required to obtain population size estimates and their accuracy. Species and population characteristics influence the ease of obtaining population estimates and the accuracy of those estimates. You will choose a method of population estimation and manipulate the amount of effort, to explore the effects on estimate accuracy.

9. Density-Dependent and Density-Independent Factors: This Web exercise explores the effects of density-dependent and density-independent factors on populations. You will analyze data from populations of arctic ground squirrels to determine these effects on weaning success, over-wintering survival, and population growth rate.

10. Population Dynamics: This Web exercise explores how changes in population growth rates and the extent of delayed density dependence affect population dynamics. You will manipulate the values of these two factors, and run a simulation to determine their effects on a population.

11. Character Displacement: This Web exercise explores character displacement and phenotypic plasticity for a polyphenism in a spadefoot toad species. You will interpret data collected on different populations of toads and the results of common garden experiments to assess genetic effects.

12. Cascading Effects of Predators: This Web exercise explores the effect of predators through multiple trophic levels. You will read a recent paper on predator-driven cascades in marine systems. You will then use data from a system in which wolves are the top predator to test for a trophic cascade.

13. Dynamics of Disease: This Web exercise explores the dynamics of host–pathogen systems. You will manipulate traits of the interacting species to simulate various strategies of hosts and pathogens. You will also explore the spread or decline of pathogens based on the population size of vulnerable hosts, and discuss the ecological and evolutionary implications of parasitic interactions.

14. Population Dynamics of a Mutualism: This Web exercise explores the dynamics of a mutualism between cacti and moths. You will read a recent paper that presents a model of this mutualism and discusses the natural history of the two species. Using the model, you will explore the effects of starting size and proportion of the two species on population dynamics.

15. Measuring Marine Species Diversity: This Web exercise explores various methods of measuring species diversity. You will interpret data from a recent paper that measured marine species diversity, with emphasis on the benthic fauna of the continental shelf of Norway, using the Shannon index as well as other indices of diversity.

16. Soil Invertebrates and Succession: This Web exercise explores how invertebrates that live in the soil could affect patterns of succession. You will interpret data from a recent paper that shows the effects of soil invertebrates on the growth of early- and mid-succession plants.

17. Island Biogeography: This Web exercise explores the factors that determine the number of species that can live on different islands according to the theory of island biogeography. In a series of simulations, you will manipulate the size of an island and the distance from the island to the mainland to demonstrate how these factors affect the equilibrium number of species on that island.

18. Periodic Disturbance and Its Effect on Species: This Web exercise demonstrates how periodic disturbance can maintain species in a community that otherwise could not coexist. You will manipulate the frequency and intensity of disturbances to investigate this effect.

19. Drought Reduces Productivity across Europe: This Web exercise examines the effect of the 2003 European drought on primary productivity. You will interpret data from a recent paper that demonstrated that the drought did substantially reduce primary productivity at various sites in Europe.

20. Trophic Efficiency in a Coral Reef System: This Web exercise explores energy flow and efficiency of energy transfer in a coral reef community. You will read a recent paper that quantifies energy flows through multiple trophic levels in a community. Using data from the paper, you will calculate efficiencies of various steps in this system, and discuss the effects of trophic level on energy flow.

21. Dry Decomposition: This Web exercise explores how plant litter decomposes in a dry climate. You will interpret data from a recent paper demonstrating the factors responsible for litter decomposition in a semi-arid ecosystem in Patagonia.

22. Population Augmentation and Recovery of Endangered Species: This Web exercise explores the consequences of augmenting populations of endangered species with captive-raised individuals. You will read a recent paper on population augmentation in an endangered butterfly. Then, using a transition matrix model, you will explore the relative costs and benefits of population augmentation and habitat enhancement for an endangered fish, the June sucker.

23. Patch Movement: Crickets vs. Cybercrickets: This Web exercise explores how organisms move across patches in the landscape. You will interpret data from a recent paper that simulated the movement of virtual organisms between patches across landscapes with different levels of connectivity, and then compared the simulation results to results from manipulation studies. Do real crickets move like cybercrickets?

24. Nitrogen Cycle: Too Much or Too Little? This Web exercise explores global flows in reactive nitrogen from anthropogenic sources. You will read a recent paper on anthropogenic transformation of the global nitrogen cycle. You will then calculate gains and losses of nitrogen on a continental scale and discuss the potential effects on humans and the natural environment.

ECOLOGY

Second Edition

For Debra and Hannah, with thanks and love.

MLC

For Jen, Gordon, and Miles and their unending patience,
and to my students for pushing me as much as I pushed them.

WDB

For my family and my students, whose gift of time has
made all the difference.

SDH

About the Authors

MICHAEL L. CAIN, having opted to change careers and focus full-time on writing, is currently affiliated with Bowdoin College. After receiving his Ph.D. in Ecology and Evolutionary Biology from Cornell University, he taught at New Mexico State University and the Rose-Hulman Institute of Technology. In addition to his work on this book, Dr. Cain is a coauthor of Campbell's *Biology*, Ninth Edition. He has instructed students across a wide range of subjects, including introductory biology, ecology, field ecology, evolution, botany, mathematical biology, and biostatistics. His research interests include: plant ecology; long-distance dispersal; ecological and evolutionary dynamics in hybrid zones; and search behavior in plants and animals.

WILLIAM D. BOWMAN is a Professor at the University of Colorado at Boulder, affiliated with the Department of Ecology and Evolutionary Biology and the Institute of Arctic and Alpine Research. He earned his Ph.D. from Duke University. Dr. Bowman has taught courses in introductory ecology, plant ecology, plant–soil interactions, and ecosystems ecology, and has directed undergraduate summer field research programs. He is coeditor of *Structure and Function of an Alpine Ecosystem, Niwot Ridge, Colorado* (Oxford University Press, 2001). His research focuses on plant ecology, biogeochemistry, and community dynamics, and has been supported by the National Science Foundation, the Environmental Protection Agency, the National Park Service, and the Andrew W. Mellon Foundation.

SALLY D. HACKER is Associate Professor at Oregon State University, Corvallis, where she has been a faculty member since 2004. As a community ecologist interested in natural and managed coastal, dune, and estuarine communities, Dr. Hacker's research explores the structures, functions, and services of communities under varying contexts of species interactions and physical conditions. She teaches courses in introductory ecology, community ecology, and marine biology. Dr. Hacker received her Ph.D. in 1996 from Brown University, where she conducted research on the role of positive interactions in communities. This work, conducted in salt marsh systems, has been widely cited and featured in a number of ecology textbooks.

Preface

It was a joy to write this Second Edition because we love what we are writing about, ecology. Indeed, this is an exciting and challenging time to study ecology. New discoveries are pouring in, revealing factors that affect local communities and link ecosystems to one another across broad geographic areas. The progress in these and other areas of ecology could not come at a better time: Ecologists are increasingly being asked to apply their knowledge toward efforts to solve current environmental problems and prevent future ones.

Developments such as these fuel the excitement that grips the field of ecology—but they also mean that what we know about ecology is increasing very rapidly. The explosion of ecological information makes ecology a daunting subject, both to study and to teach. Students need to master a heady mix of abstract concepts, experimental reasoning, mathematical equations, and details about particular organisms and their habitats. For their part, instructors are faced with the challenge of conveying fundamental concepts, new discoveries, and the relevance and rigor of modern ecology—all in a manner that works well for students taking their first course in ecology. With these challenges in mind, the overarching goal for the Second Edition of *Ecology* was to enhance the book as a learning tool for students and as a teaching tool for professors. In setting out to achieve this goal, the book's two core principles guided our every step.

Core Principles of *Ecology*, Second Edition

This book is written for undergraduate students of ecology. We set out to introduce our readers to the beauty and importance of ecology, and to do so without boring them or overwhelming them with unnecessary detail. This is a tall order, and so when we began writing the Second Edition of *Ecology*, we kept our focus on the two core principles of this book: **"Teaching comes First!"** and **"Less is More!"**

Teaching truly does come first in *Ecology*—it motivates everything we did. The structure and content of our chapters is designed primarily to make them good tools for teaching. For example, to introduce the material covered and capture student interest, each chapter begins with a story (a "Case Study," as described more fully below) about an applied problem or interesting bit of natural history. Once students are drawn in by the Case Study, the "storyline" that begins there is maintained throughout the rest of the chapter. We use a narrative writing style to link the sections of the chapter to one another, thus helping students keep the big picture in mind. In addition, the sections of the chapter are organized around a small number of Key Concepts (also described more thoroughly below) that were carefully selected to summarize current knowledge and provide students with a clear overview of the subject at hand. Similarly, when designing the art, pedagogy came first: Many students are visual learners, so we worked very hard to ensure that each figure "tells a story" that can be understood on its own, without reference to the main body of the text.

As another way to help us achieve our primary goal of teaching students, we followed a "less is more" philosophy. We were guided by the principle that if we covered less material—but presented it clearly and well—students would learn more. Hence, our chapters are relatively short and they are built around a small number of Key Concepts (typically, three to five). We made these choices to prevent students from being overwhelmed by long, diffuse chapters, and to allow them to master the big ideas first, then fill in the details. In addition, as we worked on the drafts of our chapters, we put our "less is more" philosophy into action by asking each other whether the text served one of the following purposes:

- Does it help to explain an essential concept?
- Does it show how the process of ecological inquiry works?
- Does it motivate readers by focusing on a key ecological application or a fascinating piece of natural history?

This approach made for some tough choices as we strove to balance the addition of new material with cuts made from the First Edition, but it enabled us to focus on teaching students what is currently known about ecology without overwhelming them with excess information.

New Features of *Ecology*, Second Edition

In striving to make *Ecology* the best teaching tool possible, we updated, replaced, or cut sections of the text as appropriate, and added several new pedagogical features. These include:

Climate Change Connection Climate change has broad ecological effects with important implications for conservation and ecosystem services. Roughly two-thirds of the Second Edition chapters now include a major climate change example, followed immediately by a sentence directing students to additional content on the Companion Website. These web-based *Climate Change Connections* discuss how the example in the text connects to other levels of the ecological hierarchy, while enriching the student's understanding of ongoing climate change.

Ecological Toolkits A number of chapters include an *Ecological Toolkit*, a type of box that describes ecological "tools" such as experimental design, remote sensing, GIS, mark–recapture techniques, stable isotope analysis, DNA fingerprinting, and the calculation of species–area curves.

Figure Legend Questions Each chapter includes 3–6 *Figure Legend Questions* that are highlighted in color at the end of the legend. These questions encourage students to grapple with the figure and make sure they understand its content. The questions range from those that test whether students understand the axes or other simple aspects of the figure to those that ask students to develop or evaluate hypotheses.

In-Class Exercises For the Second Edition, a new type of inquiry exercise has been added to the Instructor's Resource Library: ready-to-go problems that take about 10 minutes to do and can be used in class or assigned as homework. One or more of these exercises has been added for each chapter.

Error Bars Where appropriate, error bars have been added to figures. To provide support for students related to this change, the Web Stats Review now includes new material on the relationship between the standard deviation and the standard error of the mean, as well as confidence intervals and linear regression.

Hallmark Features of *Ecology*

We've also revised and strengthened the following key pedagogical features of *Ecology*, introduced in the First Edition:

Pedagogical Excellence Students taking their first course in ecology are exposed to a great deal of material, on a conceptual as well as individual-systems level. To help them manage this vast amount of information, each chapter of *Ecology* is organized around a small number of Key Concepts that provide up-to-date summaries of fundamental ecological principles. All of these Key Concepts are listed on the book's back end papers.

Case Studies Each chapter opens with an interesting vignette—a *Case Study*. By presenting an engaging story or interesting application, the *Case Study* captures the reader's attention while introducing the topic of the chapter. Later, the reader is brought full circle with the corresponding "*Case Study Revisited*" section at chapter's end. Each *Case Study* relates naturally to multiple levels of the ecological hierarchy, thereby providing a nice lead-in to the *Connections in Nature* feature, described next.

Connections in Nature In most ecology textbooks, connections among levels of the ecological hierarchy are discussed briefly, perhaps only in the opening chapter. As a result, many opportunities are missed to highlight for students the fact that events in natural systems *really are* interconnected. To facilitate the ability of students to grasp how events in nature are interconnected, each chapter of *Ecology* closes with a section that discusses how the material covered in that chapter affects and is affected by interactions at other levels of the ecological hierarchy. Where appropriate, these interconnections are also emphasized in the main body of the text.

Ecological Inquiry Our understanding of ecology is constantly changing due to new observations and new results from ecological experiments and models. All chapters of the book emphasize the active, inquiry-based nature of what is known about ecology. In addition, *Ecology* includes hands-on interpretative and quantitative exercises, described next.

Hands-On Problem Solving Exercises This popular feature of the Companion Website asks students to manipulate data, explore mathematical aspects of ecology in more detail, interpret results from real experiments, and analyze simple model systems using simulations. The Second Edition includes 24 revised and new *Hands-On Problem Solving Exercises*, one for each chapter of the book. These inquiry exercises can be used in two important ways: portions of them can serve as ready-to-go, five- to ten-minute problems for in-class use (e.g., with "clickers" or to stimulate class discussion), or the entire exercise can be assigned as homework.

Ecological Applications In recent years, ecologists have increasingly focused their attention on applied issues. Similarly, many students taking introductory ecology are very interested in applied aspects of ecology. Thus,

ecological applications (including conservation biology) receive great attention in this book. Discussions of applied topics are woven into each chapter, helping to capture and retain student interest.

Links to Evolution Evolution is a central unifying theme of all biology, and its connections with ecology are very strong. Yet, ecology textbooks typically present evolution almost as a separate subject. As an alternative to the standard approach, *Ecology*'s Chapter 6 is devoted to describing the joint effects of ecology and evolution. This chapter explores the ecology of evolution at both the population level and as documented in the sweeping history of life on Earth. Concepts or applications that relate to evolution are also described in many other chapters.

Art Program Many of *Ecology*'s illustrations feature "balloon captions," which tell a story that can be understood at a glance, without relying on the accompanying text. The art program is available as part of the Instructor's Resource Library (see Media and Supplements section).

Ecology Is a Work in Progress

This book, like the subject we write about, does not consist of a set of unchanging ideas and fixed bits of information. Instead, the book will develop and change over time as we respond to new discoveries and new ways of teaching. As we roll up our sleeves to begin working on the next edition, we would love to hear from you—what you like about the book, what you don't like, and any questions or suggestions you may have for how we can improve the book. You can reach us individually or as a group by sending an email message to ecology@sinauer.com, or by writing us at *Ecology*, Sinauer Associates, 23 Plumtree Road, Sunderland, MA 01375.

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We'd like to thank some of the many people who helped us turn our ideas into a book in print. Special thanks to Mary Santelmann at Oregon State University, who read every chapter in page proofs and helped us catch lingering problems. We are grateful to all of our colleagues who generously critiqued the plan for the book or read one or more chapters in manuscript, who are listed on the following pages. Among the hundreds of people we contacted while researching this book, we also wish to thank the following individuals for their special efforts in providing guidance and generously sharing their time and expertise: Jocelyn Aycrigg, Jon Evans, Jenifer Hall-Bowman, John Jaenike, Justin Kitzes, Scott Ling, Nathan Stephenson, Debra VamVikites, and Ophelia Wang.

Finally, we would like to express our appreciation to some of our colleagues at Sinauer Associates, with whom we worked closely during the writing but especially during the book's production. Andy Sinauer supported the plan for the book from Day One. He enthusiastically participated in every phase along the way. Kathaleen Emerson and Laura Green did a terrific job guiding the book through its many stages of production. Norma Roche did a superb job of copyediting our manuscript, often encouraging us to expand certain topics or omit others to help us meet the goals outlined above. Elizabeth Morales provided the beautiful illustrations in the book and her queries always helped us sharpen the visual messages. David McIntyre, our photo editor, always managed to find exquisite images that enhance the information in the figures. Joan Gemme stayed with us through several rounds of page design. We love her final version that you see here as well as her elegant cover design. Susan McGlew coordinated the more than 100 reviews of the manuscript with great perseverance. Dean Scudder masterminded the entire marketing effort and Marie Scavotto produced the attractive brochure. Jason Dirks pulled together the impressive array of supplementary materials listed on page xiii. And Mark Belk (Brigham Young University), Charlene D'Avanzo (Hampshire College), Christiane I. M. Healey (University of Massachusetts, Amherst), Norman Johnson (University of Massachusetts, Amherst), and Amy McEuen (University of Illinois, Springfield) also demonstrated their great skill and breadth in writing the online and instructor resources.

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February 2011

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Media & Supplements to Accompany *Ecology*, Second Edition

For the Student

Companion Website (sites.sinauer.com/ecology2e)

The *Ecology* Companion Website offers students a wealth of study and review material, all available free of charge. Climate Change Connections and Web Extensions expand on the coverage of selected topics introduced in the textbook. Hands-On Problem Solving Exercises provide practical experience working with experimental data and interpreting results from simulations and models. The online quizzes (instructor registration required) are a great way for students to check their comprehension of the material covered in each chapter. And the flashcards encourage familiarity with the many new terms introduced in the ecology course.

The *Ecology*, Second Edition Companion Website includes:

- Chapter Outlines
- Chapter Summaries
- Hands-On Problem Solving Exercises
- Climate Change Connections
- Web Extensions
- Online Quizzes
- Flashcards & Key Terms
- Suggested Readings
- Web Stats Review
- Complete Glossary

(See the inside front cover for additional details.)

For the Instructor

(Available to qualified adopters)

Instructor's Resource Library

The *Ecology* Instructor's Resource Library includes a variety of resources to aid instructors in course planning, lecture development, and student assessment. The Resource Library includes:

- Figures & Tables: All of the line-art illustrations, photos, and tables from the textbook are provided as both high-resolution and low-resolution JPEGs, all optimized for use in lecture.
- PowerPoint Resources: Two different PowerPoint presentations are provided for each chapter of the textbook.
- Figures: All figures, photos, and tables from each chapter, with titles.
- Lecture: A complete lecture outline, including selected figures.
- In-Class Exercises: New for the Second Edition, these exercises provide instructors with ready-to-use problems and questions designed to be incorporated into the lecture.
- Hands-on Problem Solving Exercises: The exercises from the Companion Website are included in Microsoft Word format, with suggested answers.

All of the resources included in the Instructor's Resource Library are also available to instructors online, via the instructor's side of the Companion Website. (Instructor registration required.)

Test Bank

The *Ecology*, Second Edition Test Bank (included on the Instructor's Resource Library) includes a thorough set of multiple-choice questions for each chapter of the textbook. All important concepts are covered, and each

question is referenced to a specific chapter heading, concept number, and page number. The Test Bank also includes key terms lists, for use in terminology quizzes, and all of the questions from the Companion Website online quizzes. The test bank is included in the Instructor's Resource Library in two formats:

- Microsoft Word
- Wimba Diploma (software included): Diploma is a powerful, easy-to-use exam creation program that lets you quickly assemble exams using any combination of publisher-provided questions and your own questions.

Online Quizzing

The Companion Website includes online quizzes that can be assigned or opened for use by students as self-quizzes. Quizzes can be customized with any combination of the default questions and an instructor's own questions. Quiz results are stored in the online grade book. (Note: Instructors must register in order for their students to be able to take the quizzes.)

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