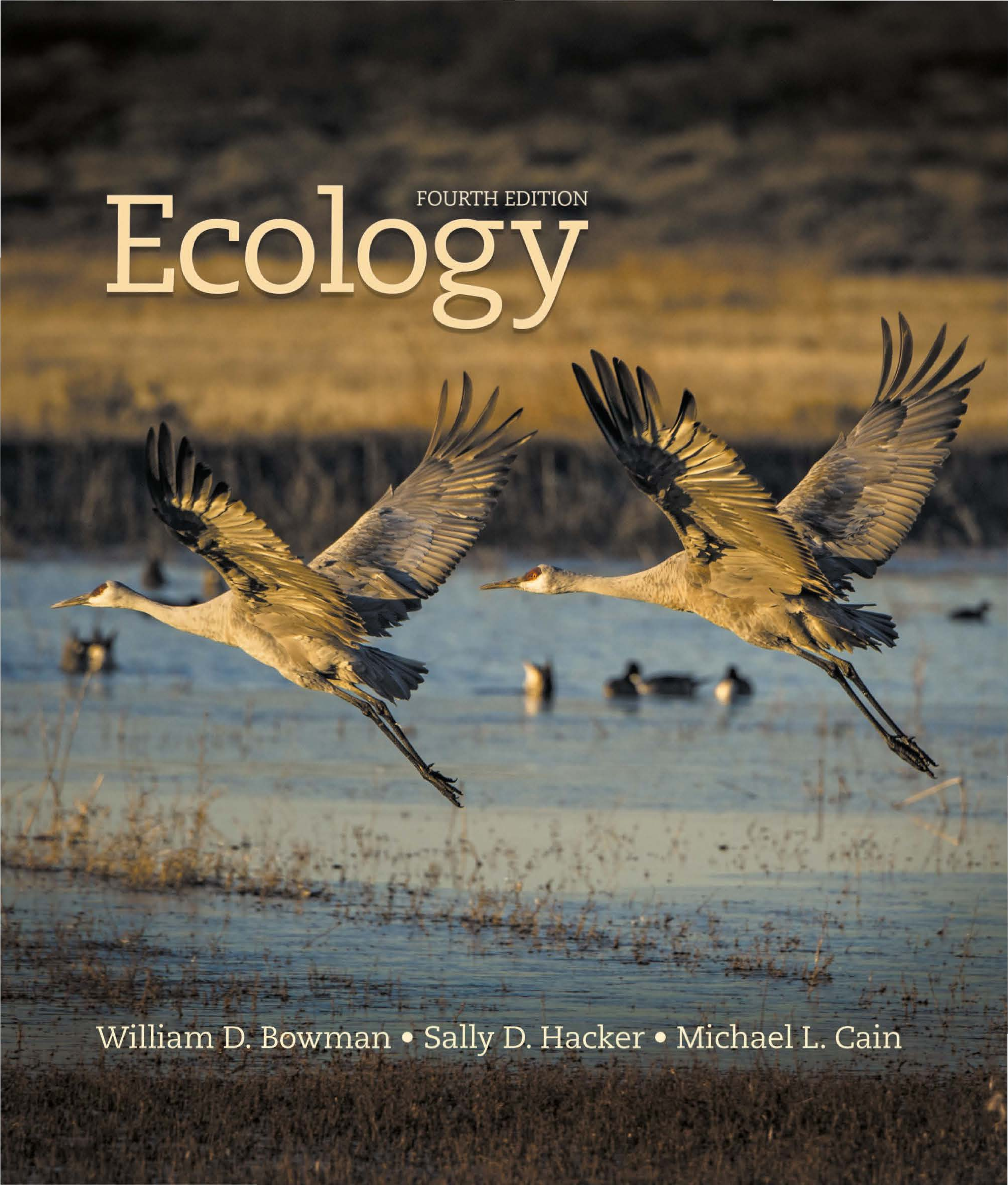
FOURTH EDITION
Ecology
William D. Bowman • Sally D. Hacker • Michael L. Cain

# Ecology Fourth Edition

# Companion Website

## ecology4e.sinauer.com

The **Ecology** website is a companion to the textbook that can help you more effectively learn and review the material covered in your ecology course. The site is designed to help you master the concepts and terminology introduced in each chapter, and to apply that knowledge to real-world problems. The site includes the following resources:

- **Web Extensions** provide expanded and additional coverage of selected topics.
- **Hands-On Problems** (example shown at right) are inquiry-based exercises that challenge you to think as a scientist, analyze and interpret experimental data, and answer questions using simulations.
- **Climate Change Connections:** Expanded for the Fourth Edition, and now featured both in the textbook and online, Climate Change Connections help you better understand climate change by relating topics introduced in the textbook to other levels of the ecological hierarchy.
- **Web Stats Review** provides a brief review of statistical methods and techniques introduced in the textbook.
- **Online Quizzes:** These multiple-choice quizzes cover all of the main topics presented in each chapter. Your instructor may assign the quizzes, or they may be made available to you as self-study tools. (Instructor registration is required for student access to the quizzes.)

**Also:** **Outlines • Summaries • Suggested Readings • Flashcards • Glossary**

**Hands-On Problem 20.1**

**20.1 The Long Hot Summer: Ecosystem Effects of the Drought of 2003 in Europe**

(This exercise is based on Ciais, Ph. and 32 others. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437: 529–533.)

**INTRODUCTION**

People living in temperate areas are accustomed to a somewhat normal cycle of dry years followed by wet years. However, the heat wave and drought that occurred in Europe in the summer of 2003 was extraordinary (**Figure 1**). It was the hottest summer on record since 1540, and it was accompanied by extreme drought.

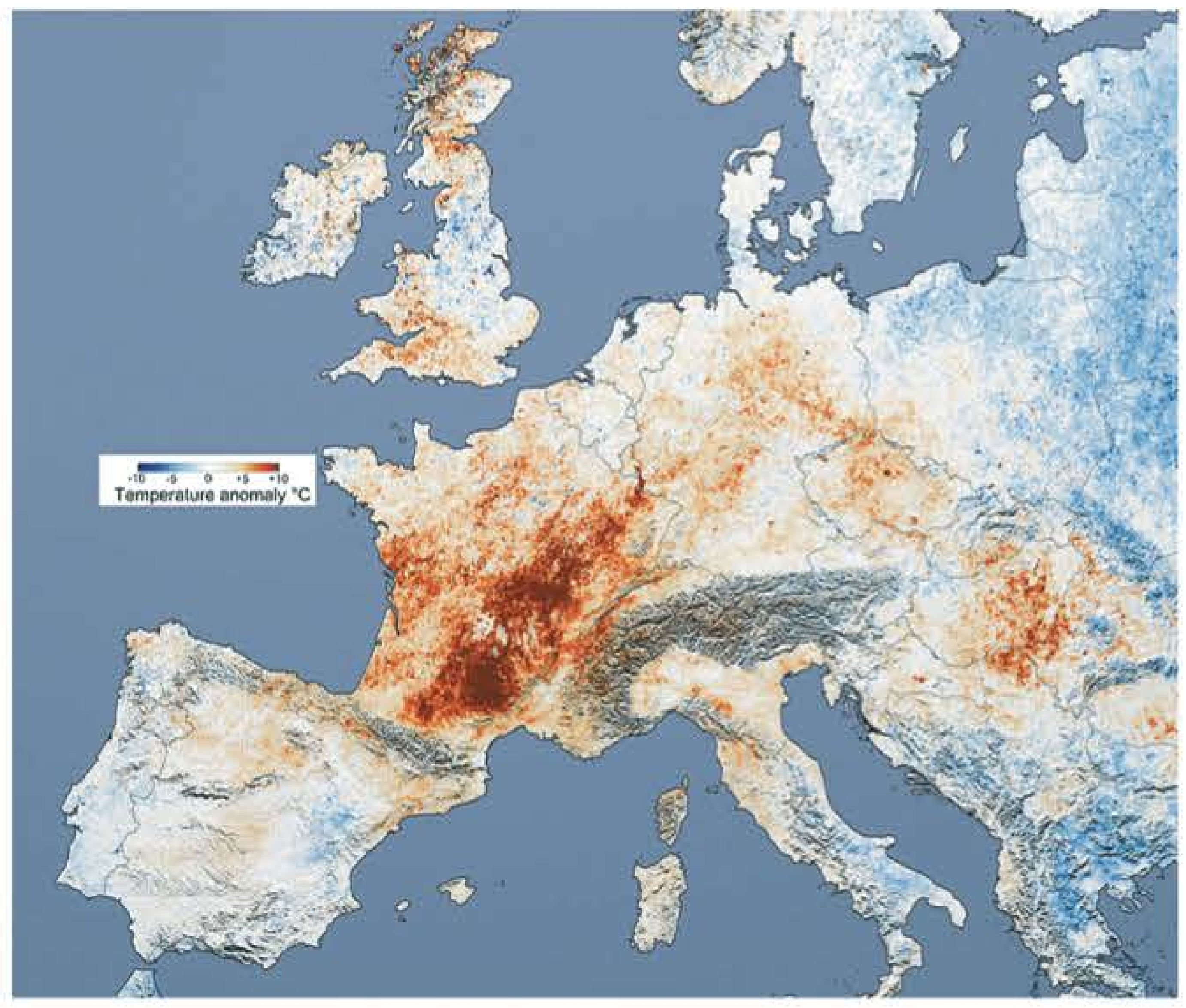


**Figure 1** Map of the temperature anomaly (variations relative to July 2001 temperatures) in Western Europe during the summer of 2003. (Image courtesy of NASA/Reto Stockli and Robert Simmon, based upon data provided by the MODIS Land Science Team)

## Access Instructions

To access the Companion Website, follow the instructions below to create an account and log in.

1. Go to **ecology4e.sinauer.com**
2. Click "Register."
3. Enter the registration code below and follow the on-screen instructions to create your account.
4. After registering, go to ecology4e.sinauer.com and log in using your newly-created login information.

**Scratch below to reveal your unique registration code:**

**Important Note:** The registration code above is valid for creating one account only.
If the code has been revealed, it may no longer be valid. New codes may be purchased at ecology4e.sinauer.com.

# Hands-On Problems

## The following Hands-On Problems are available on the Companion Website:

**1.1 When a Mosquito Flaps Its Wings...: Connections in the Natural World:** This exercise explores connections between periodic drought, mosquito populations, and the incidence of mosquito-transmitted diseases. A recent paper provides evidence that populations of mosquitos increase after severe droughts. You will consider the hypothesis that the mosquito-transmitted disease, West Nile Virus, increases after severe droughts, and discuss the implications of connections in natural systems.

**2.1 Long, Long Ago in a Galaxy not Far Away: Seasonal Climate Variation and Axial Tilt on Habitable Planets:** This exercise illustrates connections between the axial tilt of Earth and annual temperature variation. Seasonal patterns and the range of temperature variation across latitudes result from the degree of axial tilt. You will use a simulation model of Earth to vary axial tilt and explore seasonal variation in temperature across a range of latitudes.

**3.1 Advance of the Tree Lines: Biome Boundaries and Climate Change:** This exercise explores connections between elevation of tree lines and climate patterns. You will consider the results of 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 interpret plots of recent temperature changes in high elevation areas and discuss the probability of tree line advance there.

**4.1 City Ants and Country Ants: Adaptation to Thermal Environments:** This exercise explores thermal adaptation in ants that live in cities. You will interpret data from a recent paper about tolerance to high and low temperatures in ants that live in cities and ants that live in surrounding natural habitat. You will discuss the implications of the observed variation.

**5.1 Some Like it Hot: Comparison of $C_3$ and $C_4$ Pathways:** This exercise explores the conditions which favor $C_3$ or $C_4$ photosynthetic pathways. You will investigate the effects of temperature variation on growth of plants, and hypothesize about the conditions that favor alternative photosynthetic pathways. You will then test your predictions with a simulation model.

**6.1 Drifting Down the River of Life: Natural Selection and Genetic Drift:** This exercise demonstrates how natural selection and genetic drift can alter the frequencies of alleles in populations. With the use of a simulation model, you will investigate the effects of manipulating population sizes (and thus the strength of genetic drift) and the force of selection on genetic variation and persistence of variation in a population.

**7.1 "You Can't Always Get What You Want": Life History Trade-Offs:** This exercise explores the trade-off that organisms face between growth and reproduction. You will investigate the effects of manipulating the set point at which fish start allocating resources to reproduction rather than to growth under different levels of predation. You will use a simulation model to evaluate which strategies maximize fitness in differing environments.

**8.1 Eating on a Budget: Balancing Costs and Benefits of Foraging:** This exercise explores strategies predicted by optimal foraging under various conditions. Foraging decisions are based on relative costs and benefits. You will manipulate the foraging decision rules of a predator in a simulation model to explore how distance to and size of prey influence foraging strategies and resulting benefits.

**9.1 Counting Beans: Effort and Accuracy of Population Estimates:** This exercise illustrates the relationship between the effort required to obtain population size estimates and their accuracy. Species and population characteristics influence both the ease of obtaining population estimates and the accuracy of those estimates. With a simulation model, you will manipulate the amount of effort to explore the effects on estimate accuracy in two types of populations—fixed location and mobile species.

**9.2 Taking Over the World: Correlates of Cosmopolitan Distributions:** This exercise explores the species traits that promote cosmopolitan distributions of terrestrial tetrapods. You will review information from a recent paper on lineages with cosmopolitan distributions. You will consider traits that might contribute to broad distributions, and then discuss both the patterns observed and the implications of broad distributions.

**10.1 Braving the Wild Frontier: Population Dynamics in the Arctic Ground Squirrel:** This exercise explores the effects of density-dependent and density-independent factors on population growth or decline. You will compare data from populations of Arctic ground squirrels to determine the relative size of density-dependent and density-independent effects. You will compare and interpret effects on measures of reproductive success, survival, and population growth.

**10.2 Millions of Babies, but Few Children: Life Tables for Barnacles:** This exercise allows you to practice life table calculations on some classic data from barnacles. Barnacles produce millions of offspring, but few survive to adulthood. You will calculate $l_x$, $S_x$, and $F_x$, and then use these values to calculate net reproductive rate.

**11.1 Bamboo, Rats, and Famine in the Far East: Population Overshoots and Carrying Capacity:** This exercise explores how the periodic mass flowering of bamboo in southeast Asia leads to a chain of events that results in a population explosion of rats, devastation of rice crops, and widespread famine. You will use a simulation model of rat population growth to explore how the chain of events unfolds. You will manipulate carrying capacity and population growth rate to match documented changes, and then discuss the implications of population growth.

**12.1 Wolves, Willows, and the Ecology of Fear: Cascading Effects of Predators:** This exercise explores how the effects of predators can cascade through multiple trophic levels. You will review information from a recent review of predator-driven cascades in marine systems, and then use data from a study of wolves and elk to test for a trophic cascade.

**12.2 The Ups and Downs of Predators: Predator–Prey Cycles:** This exercise explores the dynamics of coupled predator/prey systems. You will use a simulation model to predict equilibrium conditions depending on characteristics of predators or prey. By manipulating the functional response and starting densities of predators and the carrying capacity and starting density of prey, you will explore joint predator/prey population dynamics and predict effects of invasive predators.

**13.1 The Animal That Changed the World: Fleas, Rats, and the Black Death:** This exercise explores the dynamics of host–pathogen systems using the Bubonic plagues of Europe as a model. You will evaluate potential scenarios for introduction of the plague to cities of a given size. You will then calculate the potential for the pathogen to spread given traits of the host and parasite, and discuss the ecological and evolutionary implications of parasitic interactions.

**14.1 If You Can't Beat 'em, and You Can't Join 'em, Move Away: Competition-Induced Character Displacement:** This exercise explores competition and possible ecological and evolutionary responses. You will review data from a recent paper on competition between two species of spadefoot toads and the development of two distinct tadpole morphologies—omnivore forms and carnivore forms—and discuss possible alternative explanations for the observed data.

**15.1 A Double-Edged Sword: Costs and Benefits of Mutualisms:** This exercise explores the dynamics of a mutualism between cacti and moths. You will review information from a recent paper that presents a model of this mutualism and discusses the natural history of the two species. Using a simulation model, you will explore the effects of starting population size and fruit abortion rate on the joint population dynamics of cacti and moths.

**16.1 "Rich without Wealth": Richness and Diversity in Marine Sediments:** This exercise explores the relationship between ecological diversity and species richness. You will use data from a recent paper on marine benthic invertebrates off the coast of Norway to compare patterns of diversity and richness among locations. You will then interpret patterns observed and discuss implications for community structure.

**16.2 Diversity, the Spice of Life: Calculating Species Diversity:** This exercise explores patterns of species diversity as affected by human impacts on the fish community in a Chilean river. You will calculate the Shannon index for several locations and compare patterns of diversity to historical data. You will interpret patterns in light of recent human impacts.

**17.1 Starting Over in a Tropical Rainforest: Succession in Ants and Plants:** This exercise explores patterns of succession in both plants and ants in a tropical rainforest in Mexico. You will review information from two papers that document succession on clear-cut plots of various ages. You will calculate the rate of successional change and the estimated time to reach climax conditions, and discuss implications for conservation and management.

**18.1 Shining a Light on the Swiss Family Robinson: Diversity and Dynamics on Islands:** This exercise explores the factors that determine the number of species that can occupy different islands according to the equilibrium 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 interact to determine the equilibrium number of species on the island.

**18.2 Why Size Matters: Island Size and Ecosystem Function:** This exercise explores the relationship between forest fragment size and diversity and function of natural systems. You will review data from a recent study in which fragments or islands of once-continuous forest were experimentally created at different sizes. You will compare diversity and ecosystem function among fragments of different sizes and relate your findings to conservation and management.

**19.1 What Goldilocks Can Teach Us about Coexistence: The Intermediate Disturbance Hypothesis:** This exercise demonstrates how periodic disturbance allows more species to coexist in a community than otherwise would be able to as a result of competitive interactions. With a simulation model you will manipulate the frequency and intensity of disturbance to investigate the balance between competition and disturbance in determining how many species can coexist.

**19.2 Does it Really Matter? Diversity and Productivity in Grasslands:** This exercise explores the relationship between species diversity and ecosystem function in a grassland system. You will review a recent experimental study and interpret patterns of change observed with increased species diversity. You will interpret data and discuss the implications of loss of diversity in natural systems.

**20.1 The Long Hot Summer: Ecosystem Effects of the Drought of 2003 in Europe:** This exercise explores the effects of the 2003 drought in Europe on ecosystem productivity. You will review a recent paper and use data from the paper to calculate temperature and precipitation change from normal. You will explore relationships between temperature change and precipitation change and measures of ecosystem productivity.

**20.2 The Cost of Staying Alive: Nitrogen and Energy in Subalpine Plants:** This exercise explores the relationship between maintenance respiration costs and nitrogen availability. You will review information from a paper that documents the relationship between nitrogen content and respiration costs in subalpine plants. You will interpret and discuss the effect of nitrogen availability on productivity in ecosystems.

**21.1 A Pound of Flesh: Trophic Efficiency in a Coral Reef:** This exercise explores energy flow and efficiency of energy transfer in a coral reef system. You will review information from a recent paper that quantifies energy flow through multiple trophic levels in a community. Using data from the paper, you will calculate efficiencies at various levels in the system, and discuss the effect of trophic level on energy flow.

**21.2 A Safe Place for My Children: Trophic Cascades and Neighborhood Effects:** This exercise explores top-down effects of predators on community assembly of prey, with an emphasis on indirect effects. You will review information from a recent paper to interpret patterns of oviposition of aquatic insects based on the presence of predators and the proximity to predator-occupied habitats. You will then discuss the implications of indirect effects of predators on trophic cascades and energy flow.

**22.1 Breaking it Down: Decomposition in Dry Environments:** This exercise explores how plant litter decomposes in a dry climate. You will review information from a recent paper about relative effects of different factors responsible for litter decomposition in a semiarid ecosystem in Patagonia. You will interpret patterns in the data to compare the effect of light versus microorganisms in litter decomposition, and discuss implications for decomposition in other areas.

**23.1 Not Dead Yet: Recovery of Endangered Species:** This exercise explores the consequences of habitat restoration and augmentation of populations of endangered species with captive-reared individuals. You will use a transition matrix model to explore the effects of habitat restoration and population augmentation on population growth of an endangered fish, the June sucker.

**24.1 You Can't Get There from Here: Movement in Heterogeneous Landscapes:** This exercise explores how organisms move across different habitats in the landscape. You will use a simulation model to explore colonization patterns of different species in heterogeneous landscapes. You will then compare time to colonization to patterns of the connecting habitat corridor and movement traits of the species.

**25.1 Too Much of a Good Thing: Anthropogenic Effects on the Global Nitrogen Cycle:** This exercise explores global flows in reactive nitrogen from anthropogenic sources. You will review a recent paper on anthropogenic transformation of the global nitrogen cycle and then calculate gains and losses of nitrogen on a continental scale. You will then discuss the potential effects of changes in the nitrogen cycle on humans and the natural environment.

# Ecology

Fourth Edition

# Ecology
FOURTH EDITION


**William D. Bowman** • University of Colorado

**Sally D. Hacker** • Oregon State University

**Michael L. Cain** • New Mexico State University



**Sinauer Associates, Inc.** Publishers
Sunderland, Massachusetts, U.S.A.


## On the Cover

Sandhill cranes (*Grus canadensis*) take off from their night refuge from predators en route to nearby fields to forage for the day. Bosque del Apache National Wildlife Refuge, New Mexico. Photograph © William D. Bowman.

**Ecology**, Fourth Edition



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*For Jen, Gordon, and Miles and their unwavering support,*
*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*

*For Debra and Hannah, with thanks and love.*
*MLC*

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**Michael L. Cain**, having opted to focus full-time on writing, is affiliated with the Department of Biology at New Mexico State University. After receiving his Ph.D. in Ecology and Evolutionary Biology from Cornell University, he was a faculty member 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* (Eleventh Edition) and *Biology in Focus* (Second 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.

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# Preface

Ecology is at the heart of understanding our world—it serves as the glue that brings together information from a multitude of very different scientific disciplines, and it integrates this information in a way that informs us about how nature works. As our environment continues to change at an alarming rate it becomes increasingly critical that we improve our understanding of the repercussions of climate change, non-sustainable extraction of resources, the spread of invasive species, and pollution. Stewardship of resources that humanity requires—food, clean water, clean air, and many others—is best understood through the lens of ecological understanding.

Advances in ecology occur regularly, facilitated by technological and computational breakthroughs, as well as creative experimental research. This continued advancement, along with the diversity of subjects that form its basis, makes ecology a potentially daunting and complicated subject to learn and teach. Covering the breadth of ecology sufficiently in a textbook requires care so that students are not overwhelmed with the amount of material and instructors have adequate material to effectively engage students. With these challenges in mind, the overarching goal for the Fourth Edition of *Ecology* was to enhance the book as a learning tool for students and as a teaching tool for professors. To achieve these goals, the book's two core principles guided our every step.

## Core Principles Guiding *Ecology*, Fourth Edition

This book is written for undergraduate students taking their first course in ecology. We set out to introduce our readers to the beauty and importance of ecology, and to do so without presenting them with too much material or boring them with unnecessary detail. While writing the Fourth Edition of *Ecology*, we kept our focus on two core principles: **"Teaching Comes First"** and **"Less Is More."**

Enabling effective teaching is our primary goal and motivation in *Ecology*. The structure and content of our chapters are designed primarily to make them good tools for teaching. For example, to introduce the material covered and capture student interest, each chapter begins with an engaging 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 it initiates 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.

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. In addition, 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, but it enabled us to focus on teaching students what is currently known about ecology without burdening them with excessive detail.

We also recognize that many instructors are choosing to "flip" their instructional style, with an emphasis on hands-on activities during classroom time and a greater reliance on student learning of core material outside of the classroom. *Ecology* serves this purpose well with its clear, easy-to-read, and well-organized presentation of material. In addition, there are several quantitative features—Analyzing Data exercises in the text and on the companion website, Hone Your Problem-Solving Skills and Hands-On Problem Solving exercises—that can serve as the basis for hands-on exercises.

## New to *Ecology*, Fourth Edition

In striving to make *Ecology* the best teaching tool possible, we have updated, replaced, and edited sections of the text as appropriate. To accommodate the new features described below and keep the book to a manageable length, we have revised and cut some sections. The Fourth Edition includes:

**Analyzing Data Exercises** As part of their education students should become comfortable working with and analyzing data. Toward that end, we've added additional *Analyzing Data* exercises on the companion website. These online exercises give students extra practice with essential skills such as performing calculations, making graphs, designing experiments, and interpreting results.

**Climate Change Connection** Recognizing the increasing evidence for and effects of climate change on ecological systems, *Climate Change Connection* examples have been added into the main text of the book. These vignettes help students appreciate the many consequences of global climate change on the distributions and functions of organisms as well as the ecosystems they depend on. Nearly half of the chapters now include an in-text *Climate Change Connection*.

**Hone Your Problem-Solving Skills** The Fourth Edition features a new section added to the set of review questions at the end of each chapter. The *Hone Your Problem-Solving Skills* questions expose students to hypothetical situations or existing data sets, and allow them to work through data analysis and interpretation to better understand key ecological concepts and relate these concepts to real life situations.

## Hallmark Features

In addition to the changes we just described, we've revised and strengthened the key pedagogical features of *Ecology*, introduced in previous editions:

**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.

**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 to multiple levels of 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.

**Online Climate Change Connection** Climate change has broad ecological effects with important implications for conservation and ecosystem services. Half of the Fourth Edition chapters include an online climate change example. These *Climate Change Connection* vignettes link topics in the text to other levels of the ecological hierarchy, while enriching the student's understanding of ongoing climate change.

**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. This occurs throughout the narrative and is further highlighted by the *Analyzing Data* exercises discussed earlier, and by the *Figure Legend Questions* (described below). In addition, *Ecology* includes a similar online *Analyzing Data* exercise for every in-text *Analyzing Data* exercise, and 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. Each chapter of the book includes one or more *Hands-On Problems*. These inquiry exercises can be used in two important ways: assigned as homework (all are available to students via the Companion Website), or used as in-class exercises (each is provided in a new instructor format that makes it easy to incorporate them into classroom sessions as active learning exercises or discussion topics).

**Figure Legend Questions** Each chapter includes 3–6 *Figure Legend Questions* that appear in maroon type 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.

**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.

**Ecological Toolkits** Nearly half of the chapters include an *Ecological Toolkit*, a box inset in the chapters 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.

**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, the first chapter of *Ecology*'s Unit 2 (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. Other topics in evolutionary ecology are explored in Chapter 7 (*Life History*) and in Chapter 8 (*Behavioral Ecology*). 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).

## 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. 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, PO Box 407, Sunderland, MA 01375 USA.

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## to accompany *Ecology*, Fourth Edition

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(ISBN 978-1-60535-619-8)

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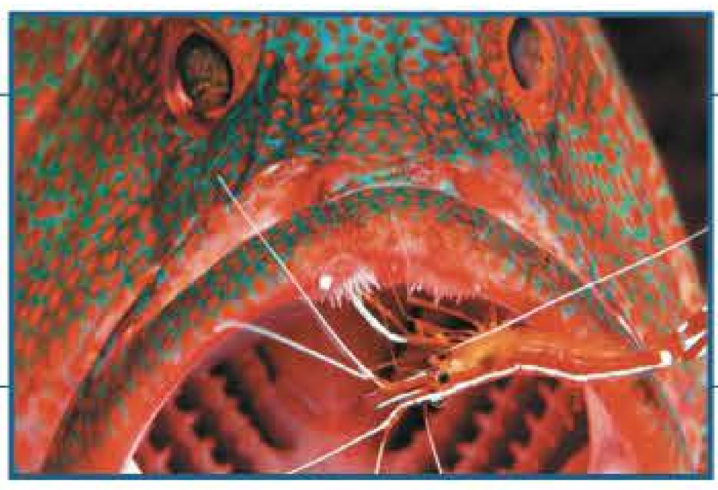


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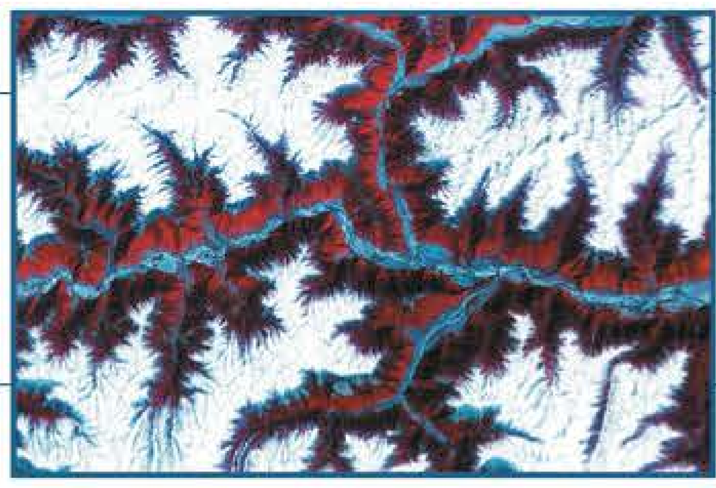

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