

ELEMENTS OF

# Ecology

Ninth Edition



Thomas M. Smith

| Robert Leo Smith





ELEMENTS OF

# Ecology

Ninth Edition

Thomas M. Smith

University of Virginia

Robert Leo Smith

West Virginia University, Emeritus

PEARSON

Boston Columbus Indianapolis New York San Francisco Upper Saddle River  
Amsterdam Cape Town Dubai London Madrid Milan Munich Paris Montréal Toronto  
Delhi Mexico City São Paulo Sydney Hong Kong Seoul Singapore Taipei Tokyo

Senior Acquisitions Editor: Star MacKenzie Burruto  
Project Manager: Margaret Young  
Program Manager: Anna Amato  
Editorial Assistant: Maja Sidzinska  
Text Permissions Project Manager: William Opaluch  
Executive Editorial Manager: Ginnie Simione-Jutson  
Program Management Team Lead: Michael Early  
Project Management Team Lead: David Zielonka  
Production Management and Compositor: Integra  
Design Manager: Derek Bacchus  
Interior and Cover Designer: Tani Hasegawa  
Illustrator: Imagineering  
Photo Permissions Management: Lumina Datamatics  
Photo Research: Steve Merland, Lumina Datamatics  
Photo Lead: Donna Kalal  
Manufacturing Buyer: Stacey Weinberger  
Executive Marketing Manager: Lauren Harp  
Cover Photo Credit: Paul Nicklen/National Geographic Creative

Credits and acknowledgments for materials borrowed from other sources and reproduced, with permission, in this textbook appear on the appropriate page within the text [or starting on p. C-1].

Copyright © 2015 Pearson Education, Inc. All rights reserved. Manufactured in the United States of America. This publication is protected by Copyright, and permission should be obtained from the publisher prior to any prohibited reproduction, storage in a retrieval system, or transmission in any form or by any means, electronic, mechanical, photocopying, recording, or likewise. To obtain permission(s) to use material from this work, please submit a written request to Pearson Education, Inc., Permissions Department, 221 River Street, Hoboken, New Jersey 07030. For information regarding permissions, call (847) 486-2635.

Many of the designations used by manufacturers and sellers to distinguish their products are claimed as trademarks. Where those designations appear in this book, and the publisher was aware of a trademark claim, the designations have been printed in initial caps or all caps.

MasteringBiology is a trademark, in the U.S. and/or other countries, of Pearson Education, Inc. or its affiliates.

#### Library of Congress Cataloging-in-Publication Data

Smith, T. M. (Thomas Michael), 1955-

Elements of ecology / Thomas M. Smith.—9th ed.

pages cm

Summary: An introductory textbook for college students.

ISBN 978-0-321-93418-5

1. Ecology. 2. Ecology—Textbooks. 3. Ecology—Study and teaching (Higher) I. Title.

QH541.S624 2015

577—dc23

2014021187

ISBN 10: 0-321-93418-0; ISBN 13: 978-0-321-93418-5 (Student edition)

ISBN 10: 0-321-99491-4; ISBN 13: 978-0-321-99491-2 (a la Carte)

**PEARSON**

www.pearsonhighered.com

1 2 3 4 5 6 7 8 9 10—V382—18 17 16 15 14



# PREFACE

The first edition of *Elements of Ecology* appeared in 1976 as a short version of *Ecology and Field Biology*. Since that time, *Elements of Ecology* has evolved into a textbook intended for use in a one-semester introduction to ecology course. Although the primary readership will be students majoring in the life sciences, in writing this text we were guided by our belief that ecology should be part of a liberal education. We believe that students who major in such diverse fields as economics, sociology, engineering, political science, law, history, English, languages, and the like should have some basic understanding of ecology for the simple reason that it has an impact on their lives.

## New for the Ninth Edition

For those familiar with this text, you will notice a number of changes in this new edition of *Elements of Ecology*. In addition to dramatic improvements to the illustrations and updating many of the examples and topics to reflect the most recent research and results in the field of ecology, we have made a number of changes in the organization and content of the text. An important objective of the text is to use the concept of adaptation through natural selection as a framework for unifying the study of ecology, linking pattern and process across the hierarchical levels of ecological study: individual organisms, populations, communities, and ecosystems. Many of the changes made in previous editions have focused on this objective, and the changes to this edition continue to work toward this goal.

## Treatment of Metapopulations

Beginning with the 7<sup>th</sup> Edition we included a separate chapter covering the topic of metapopulations (Chapter 12, 8<sup>th</sup> edition) for the first time. It was our opinion that the study of metapopulations had become a central focus in both landscape and conservation ecology and that it merited a more detailed treatment within the framework of introductory ecology. Although this chapter has consistently received high praise from reviewers, comments have suggested to us that the chapter functions more as a reference for the instructors rather than a chapter that is directly assigned in course readings. The reason for this is that most courses do not have the time to cover metapopulations as a separate subject, but rather incorporate an introduction to metapopulations in the broader context of the discussion of population structure. To address these concerns, in the 9<sup>th</sup> edition we have deleted the separate chapter on metapopulations and moved the discussion to Chapter 19: Landscape Dynamics.

## Expanded Coverage of Landscape Ecology

The incorporation of metapopulation dynamics into Chapter 19 was a part of a larger, overall revision of Landscape Dynamics in the 9<sup>th</sup> edition. Chapter 19 has been reorganized and now includes a much broader coverage of topics and presentation of current research.

## Reorganization of Materials Relating to Human Ecology

In the past three editions, the ecology of human-environment interactions has been presented in Part Eight—Human Ecology. This section of the text has been comprised of three chapters that address three of the leading environmental issues: environmental sustainability and natural resources; declining biodiversity; and climate change. The objective of these chapters was to illustrate how the science of ecology forms the foundation for understanding these important environmental issues. Based on current reviewer comments it appears that although instructors feel that the materials presented in Part Eight are important, most are not able to allocate the time to address these issues as separate topics within the constraints of a single-semester course. The question then becomes one of how to best introduce these topics within the text so that they can be better incorporated into the structure of courses that are currently being taught.

After much thought, in the 9<sup>th</sup> edition we have addressed issues of human ecology throughout the text, moving most of the topics and the materials covered in Part Eight to the various chapters where the basic ecological concepts that underlying these topics are first introduced. The topics and materials that we covered in Chapter 28 (*Population Growth, Resource Use and Environmental Sustainability*) and Chapter 29 (*Habitat Loss, Biodiversity, and Conservation*) of the 8<sup>th</sup> edition are now examined in the new feature, **Ecological Issues and Applications**, at the end of each chapter. This new feature covers a wide range of topics such as ocean acidification, plant response to elevated atmospheric carbon dioxide, the development of aquatic “dead zones” in coastal environments, sustainable resource management, genetic engineering, the consequences of habitat loss, and the conservation of threatened and endangered species.

## New Coverage of the Ecology of Climate Change

Although topics addressed in Chapters 28 and 29 of the 8<sup>th</sup> edition are now covered throughout the text in the **Ecological Issues and Applications** sections, the topic of global climate change (Chapter 30, 8<sup>th</sup> edition) is addressed in a separate chapter – Chapter 27 (The Ecology of Climate Change) in the 9<sup>th</sup> edition. Given the growing body of ecological research relating to recent and future projected climate change, we feel that it is necessary to cover this critical topic in an organized fashion within the framework of a separate chapter. This new chapter, however, is quite different from the chapter covering this topic in the 8<sup>th</sup> edition, which examined an array of topics relating to the greenhouse effect, projections of future climate change, and the potential impacts on ecological systems, agriculture, coastal environments and human health. In the 9<sup>th</sup> edition we have focused on the ecology of climate change, presenting research that examines the response of ecological



systems (from individuals to ecosystems) to recent climate change over the past century, and how ecologists are trying to understand the implications of future climate change resulting from human activities.

## Updated References and Research Case Studies to Reflect Current Ecological Research

It is essential that any science textbook reflect the current advances in research. On the other hand, it is important that they to provide an historical context by presenting references to the classic studies that developed the basic concepts that form the foundation of their science. In our text we try to set a balance between these two objectives, presenting both the classic research studies that established the foundational concepts of ecology, and presenting the new advances in the field. In the 9<sup>th</sup> edition we have undertaken a systematic review of the research and references presented in each chapter to make sure that they reflect the recent literature. Those familiar with the 8<sup>th</sup> edition will notice significant changes in the research case studies presented in each chapter.

## Updated Field Studies

The *Field Studies* features function to introduce students to actual scientists in the field of ecology, allowing the reader to identify with individuals that are conducting the research that is presented in text. The body of research presented also functions to complement the materials/subjects presented in the main body of the chapter. In the 9<sup>th</sup> edition we have updated references for the researchers who were profiled in the 8<sup>th</sup> edition. In addition, two new Field Studies features have been added to Chapter 5 (Adaptation and Natural Selection) and Chapter 8 (Properties of Populations). These two new features profile scientists whose research is in the new and growing fields of ecological genetics.

## Redesign of Art Program

For the 9<sup>th</sup> edition, the entire art program was revised to bring a consistent and updated presentation style throughout the text, with the added benefit of using color to highlight and clarify important concepts.

## Structure and Content

The structure and content of the text is guided by our basic belief that: (1) the fundamental unit in the study of ecology is the individual organism, and (2) the concept of adaptation through natural selection provides the framework for unifying the study of ecology at higher levels of organization: populations, communities, and ecosystems. A central theme of the text is the concept of trade-offs—that the set of adaptations (characteristics) that enable an organism to survive, grow, and reproduce under one set of environmental conditions inevitably impose constraints on its ability to function (survive, grow, and reproduce) equally well under different environmental conditions. These environmental conditions include both the

physical environment as well as the variety of organisms (both the same and different species) that occupy the same habitat. This basic framework provides a basis for understanding the dynamics of populations at both an evolutionary and demographic scale.

The text begins with an introduction to the science of ecology in Chapter 1 (The Nature of Ecology). The remainder of the text is divided into eight parts. Part One examines the constraints imposed on living organisms by the physical environment, both aquatic and terrestrial. Part Two begins by examining how these constraints imposed by the environment function as agents of change through the process of natural selection, the process through which adaptations evolve. The remainder of Part Two explores specific adaptations of organisms to the physical environment, considering both organisms that derive their energy from the sun (autotrophs) and those that derive their energy from the consumption and break-down of plant and animal tissues (heterotrophs).

Part Three examines the properties of populations, with an emphasis on how characteristics expressed at the level of the individual organisms ultimately determine the collective dynamics of the population. As such, **population dynamics are viewed as a function of life history** characteristics that are a product of evolution by natural selection. Part Four extends our discussion from interactions among individuals of the same species to interactions among populations of different species (interspecific interactions). In these chapters we expand our view of adaptations to the environment from one dominated by the physical environment, to the role of species interactions in the process of natural selection and on the dynamics of populations.

Part Five explores the topic of ecological communities. This discussion draws upon topics covered in Parts Two through Four to examine the factors that influence the distribution and abundance of species across environmental gradients, both spatial and temporal.

Part Six combines the discussions of ecological communities (Part Five) and the physical environment (Part One) to develop the concept of the ecosystem. Here the focus is on the flow of energy and matter through natural systems. Part Seven continues the discussion of communities and ecosystems in the context of biogeography, examining the broad-scale distribution of terrestrial and aquatic ecosystems, as well as regional and global patterns of biological diversity. The book then finishes by examining the critical environmental issue of climate change, both in the recent past, as well as the potential for future climate change as a result of human activities.

Throughout the text, in the new feature, **Ecological Issues & Applications**, we examine the application of the science of ecology to understand current environmental issues related to human activities, addressing important current environmental issues relating to population growth, sustainable resource use, and the declining biological diversity of the planet. The objective of these discussions is to explore the role of the science of ecology in both understanding and addressing these critical environmental issues.

Throughout the text we explore the science of ecology by drawing upon current research, providing examples that enable



the reader to develop an understanding of species natural history, the ecology of place (specific ecosystems), and the basic process of science.

## Associated Materials

### Personalize Learning with MasteringBiology®

[www.masteringbiology.com](http://www.masteringbiology.com)

- **New! MasteringBiology** is an online homework, tutorial, and assessment product that improves results by helping students quickly master concepts. Students benefit from self-paced tutorials that feature immediate wrong-answer feedback and hints that emulate the office-hour experience to help keep students on track. With a wide range of interactive, engaging, and assignable activities, students are encouraged to actively learn and retain tough course concepts. Specific features include:
  - **MasteringBiology assignment options reinforce basic ecology concepts presented in each chapter for students to learn and practice outside of class.**
  - **A wide variety of assignable and automatically-graded Coaching Activities**, including **GraphIt**, **QuantifyIt**, and **InvestigateIt** activities, allow students to practice and review key concepts and essential skills.
  - **MapMaster™ Interactive map activities** act as a mini-GIS tool, allowing students to layer thematic maps for analyzing patterns and data at regional and global scales. Multiple-choice and short-answer assessment questions are organized around the themes of ecosystems, physical environments, and populations.
  - **Reading Questions** keep students on track and allow them to test their understanding of ecology concepts.

## Instructor's Resource DVD for Elements of Ecology

0321977947 / 9780321977946

The Instructor Resource DVD puts all of your lecture resources in one easy-to-reach place:

- High-quality electronic versions of photos and illustrations from the book
- All of the illustrations and photos from the text presentation-ready JPEG files
- Customizable PowerPoint® lecture presentations
- Classroom Response System questions in PowerPoint
- Test Item File in Microsoft Word
- TestGen test generation and management software
- All resources are organized by chapter.

## TestGen Test Bank (Download Only) for Elements of Ecology

0321977955 / 9780321977953

TestGen is a computerized test generator that lets instructors view and edit *Test Bank* questions, transfer questions to tests, and print the test in a variety of customized formats. This *Test Bank* includes over 2,000 multiple choice, true/false, and short answer/essay questions. Questions are correlated to the revised U.S. National Geography Standards, the book's Learning Outcomes, and Bloom's Taxonomy to help teachers better map the assessments against both broad and specific teaching and learning objectives. The *Test Bank* is also available in Microsoft Word®, and is importable into Blackboard. [www.pearsonhighered.com/irc](http://www.pearsonhighered.com/irc)

## Acknowledgments

No textbook is a product of the authors alone. The material this book covers represents the work of hundreds of ecological researchers who have spent lifetimes in the field and the laboratory. Their published experimental results, observations, and conceptual thinking provide the raw material out of which the textbook is fashioned. We particularly acknowledge and thank the thirteen ecologists that are featured in the Field Studies boxes. Their cooperation in providing artwork and photographs is greatly appreciated.

Revision of a textbook depends heavily on the input of users who point out mistakes and opportunities. We took these suggestions seriously and incorporated most of them. We are deeply grateful to the following reviewers for their helpful comments and suggestions on how to improve this edition:

Bart Durham, *Lubbock Christian University*

Beth Pauley, *University of Charleston*

Bob Ford, *Frederick Community College*

Brad Basehore, *Harrisburg Area Community College*

Brian Butterfield, *Freed-Hardeman University*

Carl Pratt, *Immaculata University*

Cindy Shannon, *Mt. San Antonio College*

Claudia Jolls, *East Carolina University*

Douglas Kane, *Defiance College*

Elizabeth Davis-Berg, *Columbia College Chicago*

Emily Boone, *University of Richmond*

Fernando Agudelo-Silva, *College of Marin*

Francie Cuffney, *Meredith College*

Hazel Delcourt, *College of Coastal Georgia*

Helene Peters, *Clearwater Christian College*

James Biardi, *Fairfield University*

James Refenes, *Concordia University Ann Arbor*

John Korstad, *Oral Roberts University*

John Williams, *South Carolina State University*



Kate Lajtha, *Oregon State University*  
 Lee Rogers, *Washington State University, Tri-Cities*  
 Liane Cochran-Stafira, *Saint Xavier University*  
 Maureen Leupold, *Genesee Community College*  
 Ned Knight, *Linfield College*  
 Patricia Grove, *College of Mount Saint Vincent*  
 Peter Weishampel, *Northland College*  
 Rachel Schultz, *State University of New York at Plattsburgh*  
 Randall Tracy, *Worcester State University*  
 Rick Hammer, *Hardin-Simmons University*  
 Robert Wallace, *Ripon College*  
 Steve Blumenshine, *California State University, Fresno*  
 Tania Jogesh, *University of Illinois Urbana-Champaign*  
 Tara Ramsey, *University of Rochester*  
 Tim Tibbetts, *Monmouth College*  
 Vanessa Quinn, *Purdue University North Central*  
 Vicki Watson, *University of Montana*  
 Walter Shriner, *Mt. Hood Community College*  
 William Brown, *State University of New York at Fredonia*  
 William McClain, *Davis & Elkins College*  
 William Pearson, *University of Louisville*

## Reviewers of Previous Editions:

Steve Blumenshine, *CSU-Fresno*  
 Ned Knight, *Linfield College*  
 Brad Basehore, *Harrisburg Area Community College*  
 Kate Lajtha, *Oregon State University*  
 Claudia Jolls, *East Carolina University*  
 Randall Tracy, *Worcester State University*  
 Liane Cochran-Stafira, *Saint Xavier University*  
 Tara Ramsey, *University of Rochester*  
 Walter Shriner, *Mt. Hood Community College*  
 Patricia Grove, *College of Mount Saint Vincent*  
 William Brown, *SUNY Fredonia*  
 Bob Ford, *Frederick Community College*  
 Emily Boone, *University of Richmond*  
 Rick Hammer, *Hardin-Simmons University*  
 James Refenes, *Concordia University Ann Arbor*  
 John Williams, *South Carolina State University*  
 Randall Tracy, *Worcester State University*  
 Fernando Agudelo-Silva, *College of Marin*  
 James Biardi, *Fairfield University*

Lee Rogers, *Washington State University TriCities*  
 Maureen Leupold, *Genesee Community College*  
 Patricia Grove, *College of Mount Saint Vincent*  
 Tim Tibbetts, *Monmouth College*  
 Vanessa Quinn, *Purdue University North Central*  
 Bart Durham, *Lubbock Christian University*  
 Beth Pauley, *University of Charleston*  
 Cindy Shannon, *Mt. San Antonio College*  
 Liane Cochran-Stafira, *Saint Xavier University*  
 Peter Weishampel, *Northland College*  
 Rachel Schultz, *State University of New York at Plattsburgh*  
 Vicki Watson, *University of Montana*  
 Robert Wallace, *Ripon College*  
 Claudia Jolls, *East Carolina University*  
 Douglas Kane, *Defiance College*  
 Helene Peters, *Clearwater Christian College*  
 Kate Lajtha, *Oregon State University*  
 Tania Jogesh, *University of Illinois Urbana-Champaign*  
 William Pearson, *University of Louisville*  
 Elizabeth Davis-Berg, *Columbia College Chicago*  
 Brian Butterfield, *Freed-Hardeman University*  
 Carl Pratt, *Immaculata University*  
 Francie Cuffney, *Meredith College*  
 John Korstad, *Oral Roberts University*  
 William McClain, *Davis & Elkins College*  
 Hazel Delcourt, *College of Coastal Georgia*

The publication of a modern textbook requires the work of many editors to handle the specialized tasks of development, photography, graphic design, illustration, copy editing, and production, to name only a few. We'd like to thank the Editorial team for the dedication and support they gave this project throughout the publication process, especially acquisitions editor Star MacKenzie for her editorial guidance. Her ideas and efforts have helped to shape this edition. We'd also like to thank the rest of the team—Anna Amato, Margaret Young, Laura Murray, Jana Pratt, and Maja Sidzinska. We also appreciate the efforts of Angel Chavez at Integra-Chicago, for keeping the book on schedule.

Through it all our families, especially our spouses Nancy and Alice, had to endure the throes of book production. Their love, understanding, and support provide the balanced environment that makes our work possible.

Thomas M. Smith

Robert Leo Smith

# CONTENTS

Preface xiii

CHAPTER

1

## The Nature of Ecology 1

- 1.1 Ecology Is the Study of the Relationship between Organisms and Their Environment 2
  - 1.2 Organisms Interact with the Environment in the Context of the Ecosystem 2
  - 1.3 Ecological Systems Form a Hierarchy 3
  - 1.4 Ecologists Study Pattern and Process at Many Levels 4
  - 1.5 Ecologists Investigate Nature Using the Scientific Method 5
    - QUANTIFYING ECOLOGY 1.1: Classifying Ecological Data 7
    - QUANTIFYING ECOLOGY 1.2: Displaying Ecological Data: Histograms and Scatter Plots 8
  - 1.6 Models Provide a Basis for Predictions 10
  - 1.7 Uncertainty Is an Inherent Feature of Science 10
  - 1.8 Ecology Has Strong Ties to Other Disciplines 11
  - 1.9 The Individual Is the Basic Unit of Ecology 11
    - ECOLOGICAL ISSUES & APPLICATIONS: Ecology Has a Rich History 12
- Summary 14 • Study Questions 15  
• Further Readings 15

## PART 1 THE PHYSICAL ENVIRONMENT

CHAPTER

2

## Climate 16

- 2.1 Surface Temperatures Reflect the Difference between Incoming and Outgoing Radiation 17
- 2.2 Intercepted Solar Radiation and Surface Temperatures Vary Seasonally 19
- 2.3 Geographic Difference in Surface Net Radiation Result in Global Patterns of Atmospheric Circulation 19
- 2.4 Surface Winds and Earth's Rotation Create Ocean Currents 22
- 2.5 Temperature Influences the Moisture Content of Air 23
- 2.6 Precipitation Has a Distinctive Global Pattern 24

- 2.7 Proximity to the Coastline Influences Climate 25
  - 2.8 Topography Influences Regional and Local Patterns of Climate 26
  - 2.9 Irregular Variations in Climate Occur at the Regional Scale 27
  - 2.10 Most Organisms Live in Microclimates 28
    - ECOLOGICAL ISSUES & APPLICATIONS: Rising Atmospheric Concentrations of Greenhouse Gases Are Altering Earth's Climate 30
- Summary 33 • Study Questions 34  
• Further Readings 34

CHAPTER

3

## The Aquatic Environment 35

- 3.1 Water Cycles between Earth and the Atmosphere 36
  - 3.2 Water Has Important Physical Properties 37
  - 3.3 Light Varies with Depth in Aquatic Environments 39
  - 3.4 Temperature Varies with Water Depth 40
  - 3.5 Water Functions as a Solvent 41
  - 3.6 Oxygen Diffuses from the Atmosphere to the Surface Waters 42
  - 3.7 Acidity Has a Widespread Influence on Aquatic Environments 44
  - 3.8 Water Movements Shape Freshwater and Marine Environments 45
  - 3.9 Tides Dominate the Marine Coastal Environment 46
  - 3.10 The Transition Zone between Freshwater and Saltwater Environments Presents Unique Constraints 47
    - ECOLOGICAL ISSUES & APPLICATIONS: Rising Atmospheric Concentrations of CO<sub>2</sub> Are Impacting Ocean Acidity 48
- Summary 50 • Study Questions 51  
• Further Readings 51

CHAPTER

4

## The Terrestrial Environment 52

- 4.1 Life on Land Imposes Unique Constraints 53
- 4.2 Plant Cover Influences the Vertical Distribution of Light 54
  - QUANTIFYING ECOLOGY 4.1: Beer's Law and the Attenuation of Light 56



- 4.3 Soil Is the Foundation upon which All Terrestrial Life Depends 58
- 4.4 The Formation of Soil Begins with Weathering 58
- 4.5 Soil Formation Involves Five Interrelated Factors 58
- 4.6 Soils Have Certain Distinguishing Physical Characteristics 59
- 4.7 The Soil Body Has Horizontal Layers or Horizons 60
- 4.8 Moisture-Holding Capacity Is an Essential Feature of Soils 61
- 4.9 Ion Exchange Capacity Is Important to Soil Fertility 61
- 4.10 Basic Soil Formation Processes Produce Different Soils 62
- **ECOLOGICAL ISSUES & APPLICATIONS:**  
Soil Erosion Is a Threat to Agricultural Sustainability 64

Summary 67 • Study Questions 68  
• Further Readings 68

## PART 2 THE ORGANISM AND ITS ENVIRONMENT

### CHAPTER 5

## Adaptation and Natural Selection 69

- 5.1 Adaptations Are a Product of Natural Selection 70
- 5.2 Genes Are the Units of Inheritance 71
- 5.3 The Phenotype Is the Physical Expression of the Genotype 71
- 5.4 The Expression of Most Phenotypic Traits Is Affected by the Environment 72
- 5.5 Genetic Variation Occurs at the Level of the Population 74
- 5.6 Adaptation Is a Product of Evolution by Natural Selection 75
- 5.7 Several Processes Other than Natural Selection Can Function to Alter Patterns of Genetic Variation within Populations 78
- 5.8 Natural Selection Can Result in Genetic Differentiation 79
- **QUANTIFYING ECOLOGY 5.1:** Hardy-Weinberg Principle 80
- **FIELD STUDIES:** Hopi Hoekstra 84
- 5.9 Adaptations Reflect Trade-offs and Constraints 86
- **ECOLOGICAL ISSUES & APPLICATIONS:**  
Genetic Engineering Allows Humans to Manipulate a Species' DNA 88

Summary 90 • Study Questions 91  
• Further Readings 92

### CHAPTER 6

## Plant Adaptations to the Environment 93

- 6.1 Photosynthesis Is the Conversion of Carbon Dioxide into Simple Sugars 94
  - 6.2 The Light a Plant Receives Affects Its Photosynthetic Activity 95
  - 6.3 Photosynthesis Involves Exchanges between the Plant and Atmosphere 96
  - 6.4 Water Moves from the Soil, through the Plant, to the Atmosphere 96
  - 6.5 The Process of Carbon Uptake Differs for Aquatic and Terrestrial Autotrophs 99
  - 6.6 Plant Temperatures Reflect Their Energy Balance with the Surrounding Environment 99
  - 6.7 Constraints Imposed by the Physical Environment Have Resulted in a Wide Array of Plant Adaptations 100
  - 6.8 Species of Plants Are Adapted to Different Light Environments 101
  - **FIELD STUDIES:** Kaoru Kitajima 102
  - **QUANTIFYING ECOLOGY 6.1:** Relative Growth Rate 106
  - 6.9 The Link between Water Demand and Temperature Influences Plant Adaptations 107
  - 6.10 Plants Exhibit Both Acclimation and Adaptation in Response to Variations in Environmental Temperatures 112
  - 6.11 Plants Exhibit Adaptations to Variations in Nutrient Availability 114
  - 6.12 Plant Adaptations to the Environment Reflect a Trade-off between Growth Rate and Tolerance 116
  - **ECOLOGICAL ISSUES & APPLICATIONS:**  
Plants Respond to Increasing Atmospheric CO<sub>2</sub> 117
- Summary 120 • Study Questions 121  
• Further Readings 122

### CHAPTER 7

## Animal Adaptations to the Environment 123

- 7.1 Size Imposes a Fundamental Constraint on the Evolution of Organisms 124
- 7.2 Animals Have Various Ways of Acquiring Energy and Nutrients 127
- 7.3 In Responding to Variations in the External Environment, Animals Can Be either Conformers or Regulators 128
- 7.4 Regulation of Internal Conditions Involves Homeostasis and Feedback 129



■ **FIELD STUDIES: Martin Wikelski** 130

- 7.5 Animals Require Oxygen to Release Energy Contained in Food 132
- 7.6 Animals Maintain a Balance between the Uptake and Loss of Water 133
- 7.7 Animals Exchange Energy with Their Surrounding Environment 135
- 7.8 Animal Body Temperature Reflects Different Modes of Thermoregulation 136
- 7.9 Poikilotherms Regulate Body Temperature Primarily through Behavioral Mechanisms 137
- 7.10 Homeotherms Regulate Body Temperature through Metabolic Processes 140
- 7.11 Endothermy and Ectothermy Involve Trade-offs 141
- 7.12 Heterotherms Take on Characteristics of Ectotherms and Endotherms 142
- 7.13 Some Animals Use Unique Physiological Means for Thermal Balance 143
- 7.14 An Animal's Habitat Reflects a Wide Variety of Adaptations to the Environment 145

■ **ECOLOGICAL ISSUES & APPLICATIONS:**  
Increasing Global Temperature Is Affecting the Body Size of Animals 146

Summary 148 • Study Questions 149  
• Further Readings 150

■ **ECOLOGICAL ISSUES & APPLICATIONS:**  
Humans Aid in the Dispersal of Many Species, Expanding Their Geographic Range 167

Summary 170 • Study Questions 170  
• Further Readings 171

CHAPTER 9

## Population Growth 172

- 9.1 Population Growth Reflects the Difference between Rates of Birth and Death 173
- 9.2 Life Tables Provide a Schedule of Age-Specific Mortality and Survival 175
- **QUANTIFYING ECOLOGY 9.1: Life Expectancy** 177
- 9.3 Different Types of Life Tables Reflect Different Approaches to Defining Cohorts and Age Structure 177
- 9.4 Life Tables Provide Data for Mortality and Survivorship Curves 178
- 9.5 Birthrate Is Age-Specific 180
- 9.6 Birthrate and Survivorship Determine Net Reproductive Rate 180
- 9.7 Age-Specific Mortality and Birthrates Can Be Used to Project Population Growth 181

■ **QUANTIFYING ECOLOGY 9.2: Life History Diagrams and Population Projection Matrices** 183

- 9.8 Stochastic Processes Can Influence Population Dynamics 185
- 9.9 A Variety of Factors Can Lead to Population Extinction 185

■ **ECOLOGICAL ISSUES & APPLICATIONS:**  
The Leading Cause of Current Population Declines and Extinctions Is Habitat Loss 186

Summary 190 • Study Questions 191  
• Further Readings 191

## PART 3 POPULATIONS

CHAPTER 8

## Properties of Populations 151

- 8.1 Organisms May Be Unitary or Modular 152
- 8.2 The Distribution of a Population Defines Its Spatial Location 153
- **FIELD STUDIES: Filipe Alberto** 154
- 8.3 Abundance Reflects Population Density and Distribution 158
- 8.4 Determining Density Requires Sampling 160
- 8.5 Measures of Population Structure Include Age, Developmental Stage, and Size 162
- 8.6 Sex Ratios in Populations May Shift with Age 164
- 8.7 Individuals Move within the Population 165
- 8.8 Population Distribution and Density Change in Both Time and Space 166

CHAPTER 10

## Life History 192

- 10.1 The Evolution of Life Histories Involves Trade-offs 193
- 10.2 Reproduction May Be Sexual or Asexual 193
- 10.3 Sexual Reproduction Takes a Variety of Forms 194
- 10.4 Reproduction Involves Both Benefits and Costs to Individual Fitness 195
- 10.5 Age at Maturity Is Influenced by Patterns of Age-Specific Mortality 196
- 10.6 Reproductive Effort Is Governed by Trade-offs between Fecundity and Survival 199



## Intraspecific Population Regulation 219

- 11.1** The Environment Functions to Limit Population Growth 220  
 ■ **QUANTIFYING ECOLOGY 11.1:** Defining the Carrying Capacity ( $K$ ) 221  
 ■ **QUANTIFYING ECOLOGY 11.2:** The Logistic Model of Population Growth 222
- 11.2** Population Regulation Involves Density Dependence 222
- 11.3** Competition Results When Resources Are Limited 223
- 11.4** Intraspecific Competition Affects Growth and Development 223
- 11.5** Intraspecific Competition Can Influence Mortality Rates 225
- 11.6** Intraspecific Competition Can Reduce Reproduction 226
- 11.7** High Density Is Stressful to Individuals 228  
 ■ **FIELD STUDIES: T. Scott Sillett** 230
- 11.8** Dispersal Can Be Density Dependent 232
- 11.9** Social Behavior May Function to Limit Populations 232

Summary 217 • Study Questions 218  
 • Further Readings 218

- 10.7** There Is a Trade-off between the Number and Size of Offspring 202
- 10.8** Species Differ in the Timing of Reproduction 203  
 ■ **QUANTIFYING ECOLOGY 10.1:** Interpreting Trade-offs 204
- 10.9** An Individual's Life History Represents the Interaction between Genotype and the Environment 204
- 10.10** Mating Systems Describe the Pairing of Males and Females 206
- 10.11** Acquisition of a Mate Involves Sexual Selection 208  
 ■ **FIELD STUDIES: Alexandra L. Basolo** 210
- 10.12** Females May Choose Mates Based on Resources 212
- 10.13** Patterns of Life History Characteristics Reflect External Selective Forces 213  
 ■ **ECOLOGICAL ISSUES & APPLICATIONS:** The Life History of the Human Population Reflects Technological and Cultural Changes 215

- 11.10** Territoriality Can Function to Regulate Population Growth 233
- 11.11** Plants Preempt Space and Resources 234
- 11.12** A Form of Inverse Density Dependence Can Occur in Small Populations 235
- 11.13** Density-Independent Factors Can Influence Population Growth 237  
 ■ **ECOLOGICAL ISSUES & APPLICATIONS:** The Conservation of Populations Requires an Understanding of Minimum Viable Population Size and Carrying Capacity 239
- Summary 240 • Study Questions 241  
 • Further Readings 242

## PART 4 SPECIES INTERACTIONS

## Species Interactions, Population Dynamics, and Natural Selection 243

- 12.1** Species Interactions Can Be Classified Based on Their Reciprocal Effects 244
- 12.2** Species Interactions Influence Population Dynamics 245  
 ■ **QUANTIFYING ECOLOGY 12.1:** Incorporating Competitive Interactions in Models of Population Growth 247
- 12.3** Species Interactions Can Function as Agents of Natural Selection 247
- 12.4** The Nature of Species Interactions Can Vary Across Geographic Landscapes 251
- 12.5** Species Interactions Can Be Diffuse 252
- 12.6** Species Interactions Influence the Species' Niche 254
- 12.7** Species Interactions Can Drive Adaptive Radiation 256  
 ■ **ECOLOGICAL ISSUES & APPLICATIONS:** Urbanization Has Negatively Impacted Most Species while Favoring a Few 257
- Summary 259 • Study Questions 260  
 • Further Readings 260

## Interspecific Competition 262

- 13.1** Interspecific Competition Involves Two or More Species 263
- 13.2** The Combined Dynamics of Two Competing Populations Can Be Examined Using the Lotka–Volterra Model 263



- 13.3** There Are Four Possible Outcomes of Interspecific Competition 264
- 13.4** Laboratory Experiments Support the Lotka–Volterra Model 266
- 13.5** Studies Support the Competitive Exclusion Principle 267
- 13.6** Competition Is Influenced by Nonresource Factors 268
- 13.7** Temporal Variation in the Environment Influences Competitive Interactions 269
- 13.8** Competition Occurs for Multiple Resources 269
- 13.9** Relative Competitive Abilities Change along Environmental Gradients 271
- **QUANTIFYING ECOLOGY 13.1:** Competition under Changing Environmental Conditions: Application of the Lotka–Volterra Model 274
- 13.10** Interspecific Competition Influences the Niche of a Species 275
- 13.11** Coexistence of Species Often Involves Partitioning Available Resources 277
- 13.12** Competition Is a Complex Interaction Involving Biotic and Abiotic Factors 280
- **ECOLOGICAL ISSUES & APPLICATIONS:** Is Range Expansion of Coyote a Result of Competitive Release from Wolves? 280
- Summary 282 • Study Questions 283  
• Further Readings 284

CHAPTER

14

**Predation 285**

- 14.1** Predation Takes a Variety of Forms 286
- 14.2** Mathematical Model Describes the Interaction of Predator and Prey Populations 286
- 14.3** Predator–Prey Interaction Results in Population Cycles 288
- 14.4** Model Suggests Mutual Population Regulation 290
- 14.5** Functional Responses Relate Prey Consumed to Prey Density 291
- **QUANTIFYING ECOLOGY 14.1:** Type II Functional Response 293
- 14.6** Predators Respond Numerically to Changing Prey Density 294
- 14.7** Foraging Involves Decisions about the Allocation of Time and Energy 297
- **QUANTIFYING ECOLOGY 14.2:** A Simple Model of Optimal Foraging 298
- 14.8** Risk of Predation Can Influence Foraging Behavior 298

- 14.9** Coevolution Can Occur between Predator and Prey 299
- 14.10** Animal Prey Have Evolved Defenses against Predators 300
- 14.11** Predators Have Evolved Efficient Hunting Tactics 302
- 14.12** Herbivores Prey on Autotrophs 303
- **FIELD STUDIES: Rick A. Relyea** 304
- 14.13** Plants Have Evolved Characteristics That Deter Herbivores 306
- 14.14** Plants, Herbivores, and Carnivores Interact 307
- 14.15** Predators Influence Prey Dynamics through Lethal and Nonlethal Effects 308
- **ECOLOGICAL ISSUES & APPLICATIONS:** Sustainable Harvest of Natural Populations Requires Being a “Smart Predator” 309
- Summary 311 • Study Questions 312  
• Further Readings 313

CHAPTER

15

**Parasitism and Mutualism 314**

- 15.1** Parasites Draw Resources from Host Organisms 315
- 15.2** Hosts Provide Diverse Habitats for Parasites 316
- 15.3** Direct Transmission Can Occur between Host Organisms 316
- 15.4** Transmission between Hosts Can Involve an Intermediate Vector 317
- 15.5** Transmission Can Involve Multiple Hosts and Stages 317
- 15.6** Hosts Respond to Parasitic Invasions 318
- 15.7** Parasites Can Affect Host Survival and Reproduction 319
- 15.8** Parasites May Regulate Host Populations 320
- 15.9** Parasitism Can Evolve into a Mutually Beneficial Relationship 321
- 15.10** Mutualisms Involve Diverse Species Interactions 322
- 15.11** Mutualisms Are Involved in the Transfer of Nutrients 323
- **FIELD STUDIES: John J. Stachowicz** 324
- 15.12** Some Mutualisms Are Defensive 326
- 15.13** Mutualisms Are Often Necessary for Pollination 327
- 15.14** Mutualisms Are Involved in Seed Dispersal 328
- 15.15** Mutualism Can Influence Population Dynamics 329



- **QUANTIFYING ECOLOGY 15.1: A Model of Mutualistic Interactions** 330
- **ECOLOGICAL ISSUES & APPLICATIONS: Land-use Changes Are Resulting in an Expansion of Infectious Diseases Impacting Human Health** 331

Summary 333 • Study Questions 334  
• Further Readings 335

## PART 5 COMMUNITY ECOLOGY

### CHAPTER 16

## Community Structure 336

- 16.1 Biological Structure of Community Defined by Species Composition 337
- 16.2 Species Diversity Is defined by Species Richness and Evenness 338
- 16.3 Dominance Can Be defined by a Number of Criteria 340
- 16.4 Keystone Species Influence Community Structure Disproportionately to Their Numbers 341
- 16.5 Food Webs Describe Species Interactions 342
- 16.6 Species within a Community Can Be Classified into Functional Groups 347
- 16.7 Communities Have a Characteristic Physical Structure 347
- 16.8 Zonation Is Spatial Change in Community Structure 351
- 16.9 Defining Boundaries between Communities Is Often Difficult 352

### ■ **QUANTIFYING ECOLOGY 16.1: Community Similarity** 354

- 16.10 Two Contrasting Views of the Community 354

### ■ **ECOLOGICAL ISSUES & APPLICATIONS: Restoration Ecology Requires an Understanding of the Processes Influencing the Structure and Dynamics of Communities** 356

Summary 358 • Study Questions 358  
• Further Readings 359

### CHAPTER 17

## Factors Influencing the Structure of Communities 360

- 17.1 Community Structure Is an Expression of the Species' Ecological Niche 361
- 17.2 Zonation Is a Result of Differences in Species' Tolerance and Interactions along Environmental Gradients 363
- **FIELD STUDIES: Sally D. Hacker** 364
- 17.3 Species Interactions Are Often Diffuse 369

- 17.4 Food Webs Illustrate Indirect Interactions 371
- 17.5 Food Webs Suggest Controls of Community Structure 374
- 17.6 Environmental Heterogeneity Influences Community Diversity 376
- 17.7 Resource Availability Can Influence Plant Diversity within a Community 377
- **ECOLOGICAL ISSUES & APPLICATIONS: The Reintroduction of a Top Predator to Yellowstone National Park Led to a Complex Trophic Cascade** 380

Summary 382 • Study Questions 383  
• Further Readings 384

### CHAPTER 18

## Community Dynamics 385

- 18.1 Community Structure Changes through Time 386
- 18.2 Primary Succession Occurs on Newly Exposed Substrates 388
- 18.3 Secondary Succession Occurs after Disturbances 389
- 18.4 The Study of Succession Has a Rich History 391
- 18.5 Succession Is Associated with Autogenic Changes in Environmental Conditions 394
- 18.6 Species Diversity Changes during Succession 396
- 18.7 Succession Involves Heterotrophic Species 397
- 18.8 Systematic Changes in Community Structure Are a Result of Allogenic Environmental Change at a Variety of Timescales 399
- 18.9 Community Structure Changes over Geologic Time 400
- 18.10 The Concept of Community Revisited 401

### ■ **ECOLOGICAL ISSUES & APPLICATIONS: Community Dynamics in Eastern North America over the Past Two Centuries Are a Result of Changing Patterns of Land Use** 405

Summary 407 • Study Questions 408  
• Further Readings 408

### CHAPTER 19

## Landscape Dynamics 410

- 19.1 A Variety of Processes Gives Rise to Landscape Patterns 411
- 19.2 Landscape Pattern Is defined by the Spatial Arrangement and Connectivity of Patches 413



- 19.3** Boundaries Are Transition Zones that Offer Diverse Conditions and Habitats 415
- 19.4** Patch Size and Shape Influence Community Structure 418
- 19.5** Landscape Connectivity Permits Movement between Patches 422  
 ■ **FIELD STUDIES: Nick A. Haddad** 424
- 19.6** The Theory of Island Biogeography Applies to Landscape Patches 426
- 19.7** Metapopulation Theory Is a Central Concept in the Study of Landscape Dynamics 428  
 ■ **Quantifying Ecology 19.1: Model of Metapopulation Dynamics** 429
- 19.8** Local Communities Occupying Patches on the Landscape Define the Metacommunity 431
- 19.9** The Landscape Represents a Shifting Mosaic of Changing Communities 432  
 ■ **ECOLOGICAL ISSUES & APPLICATIONS: Corridors Are Playing a Growing Role in Conservation Efforts** 433
- Summary 436 • Study Questions 437  
 • Further Readings 438

## PART 6 ECOSYSTEM ECOLOGY

### CHAPTER

## 20

### Ecosystem Energetics 439

- 20.1** The Laws of Thermodynamics Govern Energy Flow 440
- 20.2** Energy Fixed in the Process of Photosynthesis Is Primary Production 440
- 20.3** Climate and Nutrient Availability Are the Primary Controls on Net Primary Productivity in Terrestrial Ecosystems 441
- 20.4** Light and Nutrient Availability Are the Primary Controls on Net Primary Productivity in Aquatic Ecosystems 444
- 20.5** External Inputs of Organic Carbon Can Be Important to Aquatic Ecosystems 447
- 20.6** Energy Allocation and Plant Life-Form Influence Primary Production 448
- 20.7** Primary Production Varies with Time 449
- 20.8** Primary Productivity Limits Secondary Production 450
- 20.9** Consumers Vary in Efficiency of Production 452
- 20.10** Ecosystems Have Two Major Food Chains 453  
 ■ **FIELD STUDIES: Brian Silliman** 454

### CHAPTER

## 21

### Decomposition and Nutrient Cycling 464

- 21.1** Most Essential Nutrients Are Recycled within the Ecosystem 465
- 21.2** Decomposition Is a Complex Process Involving a Variety of Organisms 466
- 21.3** Studying Decomposition Involves Following the Fate of Dead Organic Matter 468  
 ■ **QUANTIFYING ECOLOGY 21.1: Estimating the Rate of Decomposition** 469
- 21.4** Several Factors Influence the Rate of Decomposition 470
- 21.5** Nutrients in Organic Matter Are Mineralized during Decomposition 473  
 ■ **FIELD STUDIES: Edward (Ted) A. G. Schuur** 474
- 21.6** Decomposition Proceeds as Plant Litter Is Converted into Soil Organic Matter 477
- 21.7** Plant Processes Enhance the Decomposition of Soil Organic Matter in the Rhizosphere 479
- 21.8** Decomposition Occurs in Aquatic Environments 480
- 21.9** Key Ecosystem Processes Influence the Rate of Nutrient Cycling 481
- 21.10** Nutrient Cycling Differs between Terrestrial and Open-Water Aquatic Ecosystems 482
- 21.11** Water Flow Influences Nutrient Cycling in Streams and Rivers 484
- 21.12** Land and Marine Environments Influence Nutrient Cycling in Coastal Ecosystems 485
- 21.13** Surface Ocean Currents Bring about Vertical Transport of Nutrients 486



■ **ECOLOGICAL ISSUES & APPLICATIONS:**  
**Agriculture Disrupts the Process of**  
**Nutrient Cycling 487**

Summary 490 • Study Questions 491  
 • Further Readings 492

## CHAPTER 22 Biogeochemical Cycles 493

- 22.1 There Are Two Major Types of Biogeochemical Cycles 494
- 22.2 Nutrients Enter the Ecosystem via Inputs 494
- 22.3 Outputs Represent a Loss of Nutrients from the Ecosystem 495
- 22.4 Biogeochemical Cycles Can Be Viewed from a Global Perspective 495
- 22.5 The Carbon Cycle Is Closely Tied to Energy Flow 495
- 22.6 Carbon Cycling Varies Daily and Seasonally 497
- 22.7 The Global Carbon Cycle Involves Exchanges among the Atmosphere, Oceans, and Land 498
- 22.8 The Nitrogen Cycle Begins with Fixing Atmospheric Nitrogen 499
- 22.9 The Phosphorus Cycle Has No Atmospheric Pool 501
- 22.10 The Sulfur Cycle Is Both Sedimentary and Gaseous 502
- 22.11 The Global Sulfur Cycle Is Poorly Understood 503
- 22.12 The Oxygen Cycle Is Largely under Biological Control 504
- 22.13 The Various Biogeochemical Cycles Are Linked 505

■ **ECOLOGICAL ISSUES & APPLICATIONS:**  
**Nitrogen Deposition from Human**  
**Activities Can Result in Nitrogen**  
**Saturation 505**

Summary 507 • Study Questions 509  
 • Further Readings 509

## PART 7 ECOLOGICAL BIOGEOGRAPHY

### CHAPTER 23 Terrestrial Ecosystems 510

- 23.1 Terrestrial Ecosystems Reflect Adaptations of the Dominant Plant Life-Forms 512
  - 23.2 Tropical Forests Characterize the Equatorial Zone 514
- **QUANTIFYING ECOLOGY 23.1:**  
**Climate Diagrams 515**

- 23.3 Tropical Savannas Are Characteristic of Semiarid Regions with Seasonal Rainfall 517
- 23.4 Grassland Ecosystems of the Temperate Zone Vary with Climate and Geography 519
- 23.5 Deserts Represent a Diverse Group of Ecosystems 522
- 23.6 Mediterranean Climates Support Temperate Shrublands 524
- 23.7 Forest Ecosystems Dominate the Wetter Regions of the Temperate Zone 526
- 23.8 Conifer Forests Dominate the Cool Temperate and Boreal Zones 528
- 23.9 Low Precipitation and Cold Temperatures Define the Arctic Tundra 530

■ **ECOLOGICAL ISSUES & APPLICATIONS:**  
**The Extraction of Resources from**  
**Forest Ecosystems Involves an Array of**  
**Management Practices 533**

Summary 536 • Study Questions 537  
 • Further Readings 538

### CHAPTER 24 Aquatic Ecosystems 539

- 24.1 Lakes Have Many Origins 540
  - 24.2 Lakes Have Well-Defined Physical Characteristics 540
  - 24.3 The Nature of Life Varies in the Different Zones 542
  - 24.4 The Character of a Lake Reflects Its Surrounding Landscape 543
  - 24.5 Flowing-Water Ecosystems Vary in Structure and Types of Habitats 544
  - 24.6 Life Is Highly Adapted to Flowing Water 545
- **QUANTIFYING ECOLOGY 24.1:**  
**Streamflow 546**
- 24.7 The Flowing-Water Ecosystem Is a Continuum of Changing Environments 548
  - 24.8 Rivers Flow into the Sea, Forming Estuaries 549
  - 24.9 Oceans Exhibit Zonation and Stratification 551
  - 24.10 Pelagic Communities Vary among the Vertical Zones 552
  - 24.11 Benthos Is a World of Its Own 553
  - 24.12 Coral Reefs Are Complex Ecosystems Built by Colonies of Coral Animals 554



- 24.13** Productivity of the Oceans Is Governed by Light and Nutrients 556
- **ECOLOGICAL ISSUES & APPLICATIONS:** Inputs of Nutrients to Coastal Waters Result in the Development of "Dead Zones" 556

Summary 558 • Study Questions 560  
• Further Readings 560

CHAPTER  
**25**

## Coastal and Wetland Ecosystems 561

- 25.1** The Intertidal Zone Is the Transition between Terrestrial and Marine Environments 562
- 25.2** Rocky Shorelines Have a Distinct Pattern of Zonation 562
- 25.3** Sandy and Muddy Shores Are Harsh Environments 564
- 25.4** Tides and Salinity Dictate the Structure of Salt Marshes 565
- 25.5** Mangroves Replace Salt Marshes in Tropical Regions 566
- 25.6** Freshwater Wetlands Are a Diverse Group of Ecosystems 567
- 25.7** Hydrology Defines the Structure of Freshwater Wetlands 569
- 25.8** Freshwater Wetlands Support a Rich Diversity of Life 571
- **ECOLOGICAL ISSUES & APPLICATIONS:** Wetland Ecosystems Continue to Decline as a Result of Land Use 571

Summary 573 • Study Questions 574  
• Further Readings 574

CHAPTER  
**26**

## Large-Scale Patterns of Biological Diversity 575

- 26.1** Earth's Biological Diversity Has Changed through Geologic Time 576
- 26.2** Past Extinctions Have Been Clustered in Time 577
- 26.3** Regional and Global Patterns of Species Diversity Vary Geographically 578
- 26.4** Various Hypotheses Have Been proposed to Explain Latitudinal Gradients of Diversity 580
- 26.5** Species Richness Is Related to Available Environmental Energy 582
- 26.6** Large-scale Patterns of Species Richness Are Related to Ecosystem Productivity 584

- 26.7** Regional Patterns of Species Diversity Are a Function of Processes Operating at Many Scales 587

- **ECOLOGICAL ISSUES & APPLICATIONS:** Regions of High Species Diversity Are Crucial to Conservation Efforts 588

Summary 590 • Study Questions 591  
• Further Readings 591

CHAPTER  
**27**

## The Ecology of Climate Change 592

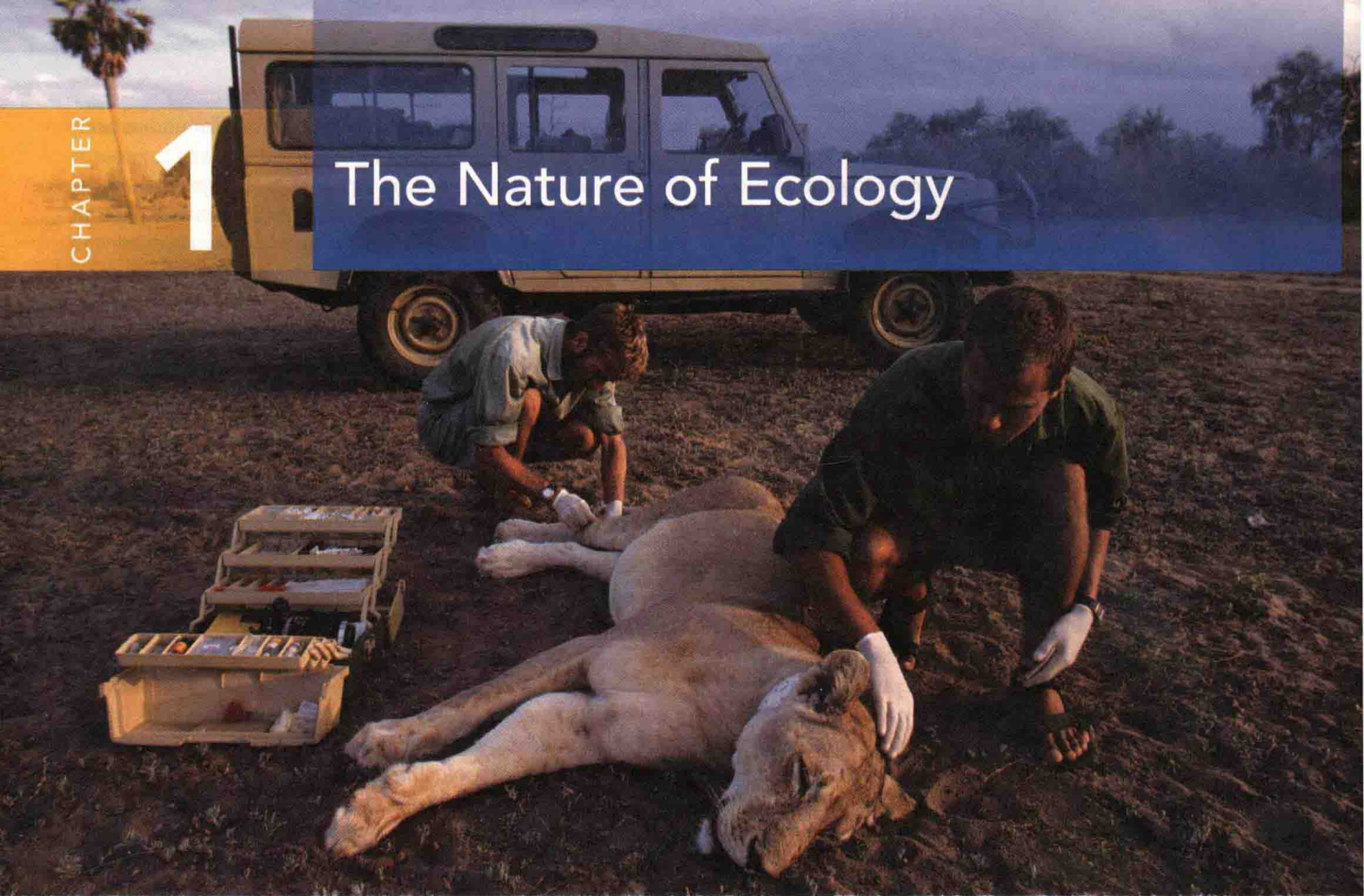
- 27.1** Earth's Climate Has Warmed over the Past Century 593
- 27.2** Climate Change Has a Direct Influence on the Physiology and Development of Organisms 595
- 27.3** Recent Climate Warming Has Altered the Phenology of Plant and Animal Species 598
- 27.4** Changes in Climate Have Shifted the Geographic Distribution of Species 599
- 27.5** Recent Climate Change Has Altered Species Interactions 602
- 27.6** Community Structure and Regional Patterns of Diversity Have Responses to Recent Climate Change 605
- 27.7** Climate Change Has Impacted Ecosystem Processes 607
- 27.8** Continued Increases in Atmospheric Concentrations of Greenhouse Gases Is Predicted to Cause Future Climate Change 608
- 27.9** A Variety of Approaches Are Being Used to Predict the Response of Ecological Systems to Future Climate Change 610
- **FIELD STUDIES:** Erika Zavaleta 612
- 27.10** Predicting Future Climate Change Requires an Understanding of the Interactions between the Biosphere and the Other Components of the Earth's System 617

Summary 619 • Study Questions 620  
• Further Readings 621

References R-1  
Glossary G-1  
Credits C-1  
Index I-1



# The Nature of Ecology



Scientists collect blood samples from a sedated lioness that has been fitted with a GPS tracking collar as part of an ongoing study of the ecology of lions inhabiting the Selous Game Reserve in Tanzania.

## CHAPTER GUIDE

- 1.1** Ecology Is the Study of the Relationship between Organisms and Their Environment
- 1.2** Organisms Interact with the Environment in the Context of the Ecosystem
- 1.3** Ecological Systems Form a Hierarchy
- 1.4** Ecologists Study Pattern and Process at Many Levels
- 1.5** Ecologists Investigate Nature Using the Scientific Method
- 1.6** Models Provide a Basis for Predictions
- 1.7** Uncertainty Is an Inherent Feature of Science
- 1.8** Ecology Has Strong Ties to Other Disciplines
- 1.9** The Individual Is the Basic Unit of Ecology

**ECOLOGICAL** Issues & Applications History