GLOBAL EDITION

Elements of ECOLOGY

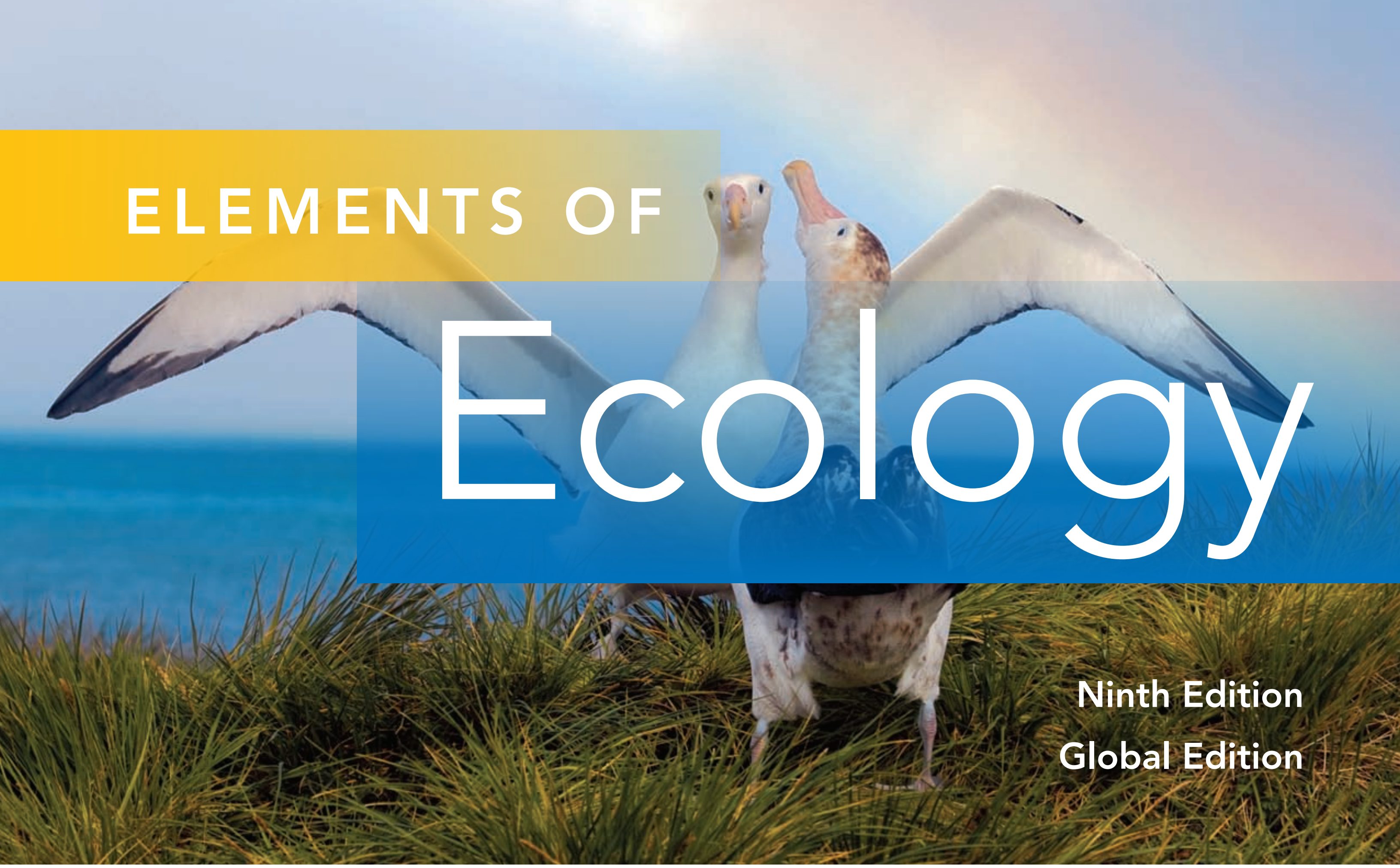
NINTH EDITION

Thomas M. Smith • Robert Leo Smith

ALWAYS LEARNING

PEARSON

BRIEF CONTENTS



ELEMENTS OF Ecology

Ninth Edition

Global 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
Publishing Administrator and Business Analyst, Global Edition: Shokhi Shah Khandelwal
Acquisitions Editor, Global Edition: Priyanka Ahuja
Assitant Project Editor, Global Edition: Sinjita Basu
Media Production Manager, Global Edition: Vikram Kumar
Senior Manufacturing Controller, Production, Global Edition: Trudy Kimber
Design Manager: Derek Bacchus
Photo Permissions Management: Lumina Datamatics
Photo Research: Steve Merland, Lumina Datamatics
Photo Lead: Donna Kalal
Manufacturing Buyer: Stacey Weinberger
Executive Marketing Manager: Lauren Harp
Full-Service Project Management: Integra
Cover Photo Source: Shutterstock
Cover Printer: CTPS China

Pearson Education Limited
Edinburgh Gate
Harlow
Essex CM20 2JE
England

and Associated Companies throughout the world

Visit us on the World Wide Web at:
www.pearsonglobaleditions.com

Authorized adaptation from the United States edition, entitled Elements of Ecology, 9th edition, ISBN 978-0-321-93418-5, by Thomas M. Smith and Robert Leo Smith, published by Pearson Education © 2015.

ISBN 10: 1-292-07740-9
ISBN 13: 978-1-292-07740-6

British Library Cataloguing-in-Publication Data
A catalogue record for this book is available from the British Library.

10 9 8 7 6 5 4 3 2 1
14 13 12 11 10

Typeset in Times LT Std 10 by Integra.

Printed and bound in China at CTPSC/01.

CONTENTS

PART 2 THE ORGANISM AND ITS ENVIRONMENT

CHAPTER 5 Adaptation and Natural Selection 85

CHAPTER 6 Plant Adaptations to the Environment 109

CHAPTER 7 Animal Adaptations to the Environment 139

CHAPTER 14

Predation 301

CHAPTER 15

Parasitism and Mutualism 330

PART 5 COMMUNITY ECOLOGY

CHAPTER 16 Community Structure 352

CHAPTER 17 Factors Influencing the Structure of Communities 376

CHAPTER 18 Community Dynamics 401

CHAPTER 19 Landscape Dynamics 426

PART 6 ECOSYSTEM ECOLOGY

CHAPTER 20 Ecosystem Energetics 455

CHAPTER 21 Decomposition and Nutrient Cycling 480

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 7th Edition we included a separate chapter covering the topic of metapopulations (Chapter 12, 8th 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 9th 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 9th 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 9th 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 8th 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 8th edition are now covered throughout the text in the **Ecological Issues and Applications** sections, the topic of global climate change (Chapter 30, 8th edition) is addressed in a separate chapter – Chapter 27 (The Ecology of Climate Change) in the 9th 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 8th 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 9th 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 9th 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 8th 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 9th edition we have updated references for the researchers who were profiled in the 8th 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 9th 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

- **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 **GraphtIt, 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.

TestGen Test Bank (Download Only) for Elements of Ecology

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.pearsonglobaleditions.com/Smith

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, *Worchester 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

Pearson wishes to thank and acknowledge the following people for their work on the Global Edition:

Contributor:

Dr. S. Jayakumar, *Pondicherry University, India*

Reviewers:

Martin Cerny, *Charles University, Prague*
Hannah Buckley, *Lincoln University, Burns*
Ahmad Tarmizi Talib, *Universiti Putra Malaysia*

CHAPTER 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

THE COLOR PHOTOGRAPH OF EARTHRISE, taken by *Apollo 8* astronaut William A. Anders on December 24, 1968, is a powerful and eloquent image (**Figure 1.1**). One leading environmentalist has rightfully described it as "the most influential environmental photograph ever taken." Inspired by the photograph, economist Kenneth E. Boulding summed up the finite nature of our planet as viewed in the context of the vast expanse of space in his metaphor "spaceship Earth." What had been perceived throughout human history as a limitless frontier had suddenly become a tiny sphere: limited in its resources, crowded by an ever-expanding human population, and threatened by our use of the atmosphere and the oceans as repositories for our consumptive wastes.

A little more than a year later, on April 22, 1970, as many as 20 million Americans participated in environmental rallies, demonstrations, and other activities as part of the first Earth Day. The *New York Times* commented on the astonishing rise in environmental awareness, stating that "Rising concern about the environmental crisis is sweeping the nation's campuses with an intensity that may be on its way to eclipsing student discontent over the war in Vietnam." Now, more than four decades later, the human population has nearly doubled (3.7 billion in 1970; 7.2 billion as of 2014). Ever-growing demand for basic resources such as food and fuel has created a new array of environmental concerns: resource use and environmental sustainability, the declining biological diversity of our planet, and the potential for human activity to significantly change Earth's climate. The environmental movement born in the 1970s continues today, and at its core is the belief in the need to redefine our relationship with nature. To do so requires an understanding of nature, and ecology is the particular field of study that provides that understanding.

1.1 Ecology Is the Study of the Relationship between Organisms and Their Environment

With the growing environmental movement of the late 1960s and early 1970s, ecology—until then familiar only to a relatively small number of academic and applied biologists—was suddenly thrust into the limelight (see this chapter, *Ecological Issues & Applications*). Hailed as a framework for understanding the relationship of humans to their environment, *ecology* became a household word that appeared in newspapers, magazines, and books—although the term was often misused. Even now, people confuse it with terms such as *environment* and *environmentalism*. Ecology is neither. Environmentalism is activism with a stated aim of protecting the natural environment, particularly from the negative impacts of human activities. This activism often takes the form of public education programs, advocacy, legislation, and treaties.

So what is ecology? Ecology is a science. According to one accepted definition, **ecology** *is the scientific study of the relationships between organisms and their environment*. That definition is satisfactory so long as one considers *relationships* and *environment* in their fullest meanings. Environment includes the physical and chemical conditions as well as the biological or living components of an organism's surroundings. Relationships include interactions with the physical world as well as with members of the same and other species.

The term *ecology* comes from the Greek words *oikos,* meaning "the family household," and *logy*, meaning "the study of." It has the same root word as *economics*, meaning "management of the household." In fact, the German zoologist Ernst Haeckel, who originally coined the term *ecology* in 1866, made explicit reference to this link when he wrote:

> By ecology we mean the body of knowledge concerning the economy of nature—the investigation of the total relations of the animal both to its inorganic and to its organic; including above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact—in a word, ecology is the study of all those complex interrelationships referred to by Darwin as the conditions of the struggle for existence.

Haeckel's emphasis on the relation of ecology to the new and revolutionary ideas put forth in Charles Darwin's *The Origin of Species* (1859) is important. Darwin's theory of natural selection (which Haeckel called "the struggle for existence") is a cornerstone of the science of ecology. It is a mechanism allowing the study of ecology to go beyond descriptions of natural history and examine the processes that control the distribution and abundance of organisms.

Figure 1.1 Photograph of Earthrise taken by *Apollo 8* astronaut William A. Anders on December 24, 1968.

1.2 Organisms Interact with the Environment in the Context of the Ecosystem

Organisms interact with their environment at many levels. The physical and chemical conditions surrounding an organism—such as ambient temperature, moisture, concentrations of oxygen and carbon dioxide, and light intensity—all influence basic physiological processes crucial to survival and growth. An organism must acquire essential resources from the surrounding environment, and in doing so, must protect itself from becoming food for other organisms. It must recognize friend from foe, differentiating between potential mates and possible predators. All of this effort is an attempt to succeed at the ultimate goal of all living organisms: to pass their genes on to successive generations.

The environment in which each organism carries out this struggle for existence is a place—a physical location in time and space. It can be as large and as stable as an ocean or as small and as transient as a puddle on the soil surface after a spring rain. This environment includes both the physical conditions and the array of organisms that coexist within its confines. This entity is what ecologists refer to as the ecosystem.

Organisms interact with the environment in the context of the **ecosystem**. The *eco*– part of the word relates to the environment. The –*system* part implies that the ecosystem functions as a collection of related parts that function as a unit. The automobile engine is an example of a system: components, such as the ignition and fuel pump, function together within the broader context of the engine. Likewise, the ecosystem consists of interacting components that function as a unit. Broadly, the ecosystem consists of two basic interacting components: the living, or **biotic**, and the nonliving (physical and chemical), or **abiotic**.

Consider a natural ecosystem, such as a forest (**Figure 1.2**). The physical (abiotic) component of the forest consists of the atmosphere, climate, soil, and water. The biotic component includes the many different organisms—plants, animals, and microbes—that inhabit the forest. Relationships are complex in that each organism not only responds to the abiotic environment but also modifies it and, in doing so, becomes part of the broader environment itself. The trees in the canopy of a forest intercept the sunlight and use this energy to fuel the process of photosynthesis. As a result, the trees modify the environment of the plants below them, reducing the sunlight and lowering air temperature. Birds foraging on insects in the litter layer of fallen leaves reduce insect numbers and modify the environment for other organisms that depend on this shared food resource. By reducing the populations of insects they feed on, the birds are also indirectly influencing the interactions among different insect species that inhabit the forest floor. We will explore these complex interactions between the living and the nonliving environment in greater detail in succeeding chapters.

1.3 Ecological Systems Form a Hierarchy

The various kinds of organisms that inhabit our forest make up populations. The term *population* has many uses and meanings in other fields of study. In ecology, a **population** is a group of individuals of the same species that occupy a given area. Populations of plants and animals in an ecosystem do not function independently of one another. Some populations compete with other populations for limited resources, such as food, water, or space. In other cases, one population is the food resource for another. Two populations may mutually benefit each other, each doing better in the presence of the other. All populations of different species living and interacting within an ecosystem are referred to collectively as a **community**.

We can now see that the ecosystem, consisting of the biotic community and the abiotic environment, has many levels (**Figure 1.3**). On one level, individual organisms both respond to and influence the abiotic environment. At the next level, individuals of the same species form populations, such as a population of white oak trees or gray squirrels within a forest. Further, individuals of these populations interact among themselves and with individuals of other species to form a community.

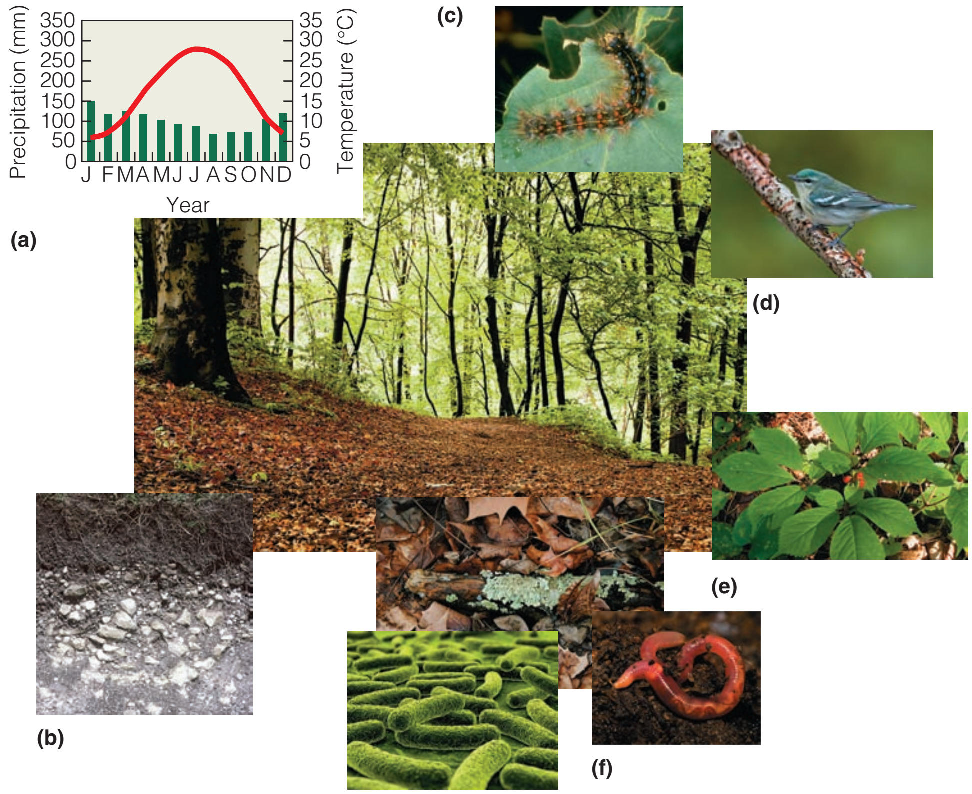


Figure 1.2 Example of the components and interactions that define a forest ecosystem. The abiotic components of the ecosystem, including the (a) climate and (b) soil, directly influence the forest trees. (c) Herbivores feed on the canopy, (d) while predators such as this warbler feed upon insects. (e) The forest canopy intercepts light, modifying its availability for understory plants. (f) A variety of decomposers, both large and small, feed on dead organic matter on the forest floor, and in doing so, release nutrients to the soil that provide for the growth of plants.

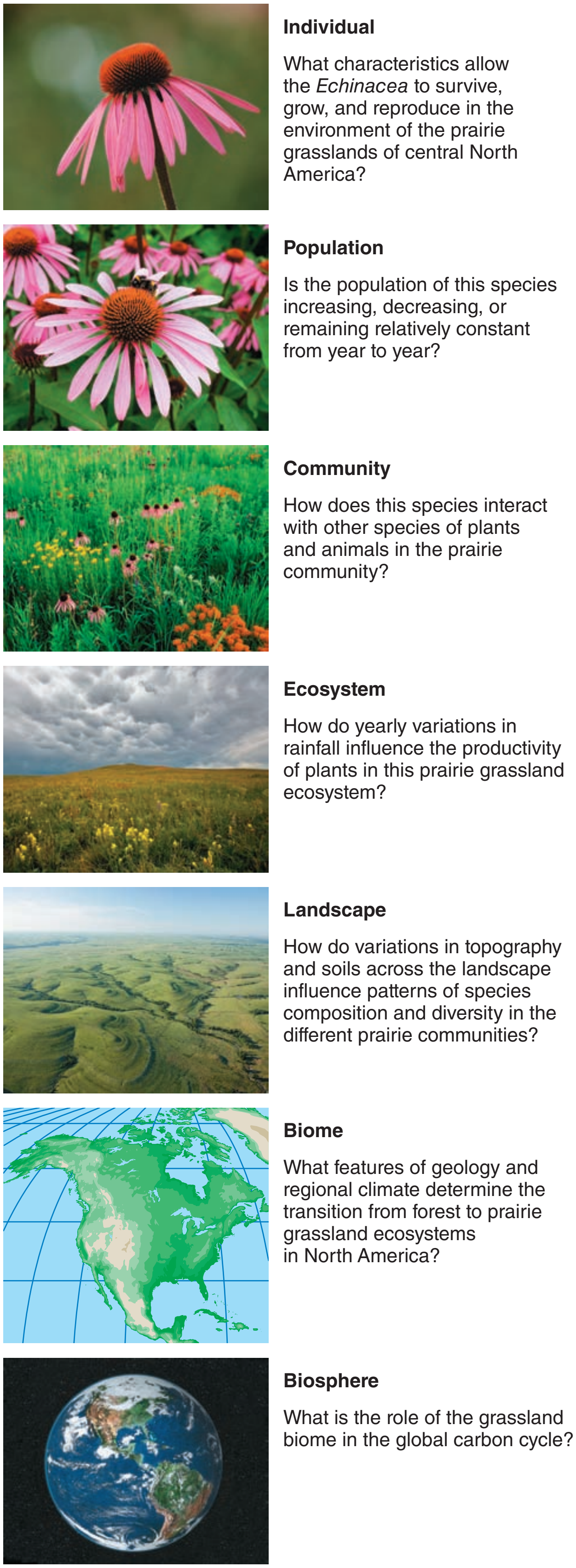


Figure 1.3 The hierarchy of ecological systems.

Herbivores consume plants, predators eat prey, and individuals compete for limited resources. When individuals die, other organisms consume and break down their remains, recycling the nutrients contained in their dead tissues back into the soil.

Organisms interact with the environment in the context of the ecosystem, yet all communities and ecosystems exist in the broader spatial context of the **landscape**—an area of land (or water) composed of a patchwork of communities and ecosystems. At the spatial scale of the landscape, communities and ecosystems are linked through such processes as the dispersal of organisms and the exchange of materials and energy.

Although each ecosystem on the landscape is distinct in that it is composed of a unique combination of physical conditions (such as topography and soils) and associated sets of plant and animal populations (communities), the broad-scale patterns of climate and geology characterizing our planet give rise to regional patterns in the geographic distribution of ecosystems (see Chapter 2). Geographic regions having similar geological and climatic conditions (patterns of temperature, precipitation, and seasonality) support similar types of communities and ecosystems. For example, warm temperatures, high rates of precipitation, and a lack of seasonality characterize the world's equatorial regions. These warm, wet conditions year-round support vigorous plant growth and highly productive, evergreen forests known as tropical rain forests (see Chapter 23). The broad-scale regions dominated by similar types of ecosystems, such as tropical rain forests, grasslands, and deserts, are referred to as **biomes**.

The highest level of organization of ecological systems is the **biosphere**—the thin layer surrounding the Earth that supports all of life. In the context of the biosphere, all ecosystems, both on land and in the water, are linked through their interactions—exchanges of materials and energy—with the other components of the Earth system: atmosphere, hydrosphere, and geosphere. Ecology is the study of the complex web of interactions between organisms and their environment at all levels of organization—from the individual organism to the biosphere.

1.4 Ecologists Study Pattern and Process at Many Levels

As we shift our focus across the different levels in the hierarchy of ecological systems—from the individual organism to the biosphere—a different and unique set of patterns and processes emerges, and subsequently a different set of questions and approaches for studying these patterns and processes is required (see Figure 1.3). The result is that the broader science of ecology is composed of a range of subdisciplines—from physiological ecology, which focuses on the functioning of individual organisms, to the perspective of Earth's environment as an integrated system forming the basis of global ecology.

Ecologists who focus on the level of the individual examine how features of morphology (structure), physiology, and behavior influence that organism's ability to survive, grow, and reproduce in its environment. Conversely, how do these same characteristics (morphology, physiology, and behavior) function to constrain the organism's ability to function successfully in other environments? By contrasting the characteristics of different species that occupy different environments, these ecologists gain insights into the factors influencing the distribution of species.

At the individual level, birth and death are discrete events. Yet when we examine the collective of individuals that make up a population, these same processes are continuous as individuals are born and die. At the population level, birth and death are expressed as rates, and the focus of study shifts to examining the numbers of individuals in the population and how these numbers change through time. Populations also have a distribution in space, leading to such questions as how are individuals spatially distributed within an area, and how do the population's characteristics (numbers and rates of birth and death) change from location to location?

As we expand our view of nature to include the variety of plant and animal species that occupy an area, the ecological community, a new set of patterns and processes emerges. At this level of the hierarchy, the primary focus is on factors influencing the relative abundances of various species coexisting within the community. What is the nature of the interactions among the species, and how do these interactions influence the dynamics of the different species' populations?

The diversity of organisms comprising the community modify as well as respond to their surrounding physical environment, and so together the biotic and abiotic components of the environment interact to form an integrated system—the ecosystem. At the ecosystem level, the emphasis shifts from species to the collective properties characterizing the flow of energy and nutrients through the combined physical and biological system. At what rate are energy and nutrients converted into living tissues (termed *biomass*)? In turn, what processes govern the rate at which energy and nutrients in the form of organic matter (living and dead tissues) are broken down and converted into inorganic forms? What environmental factors limit these processes governing the flow of energy and nutrients through the ecosystem?

As we expand our perspective even further, the landscape may be viewed as a patchwork of ecosystems whose boundaries are defined by distinctive changes in the underlying physical environment or species composition. At the landscape level, questions focus on identifying factors that give rise to the spatial extent and arrangement of the various ecosystems that make up the landscape, and ecologists explore the consequences of these spatial patterns on such processes as the dispersal of organisms, the exchange of energy and nutrients between adjacent ecosystems, and the propagation of disturbances such as fire or disease.

At a continental to global scale, the questions focus on the broad-scale distribution of different ecosystem types or biomes. How do patterns of biological diversity (the number of different types of species inhabiting the ecosystem) vary geographically across the different biomes? Why do tropical rain forests support a greater diversity of species than do forest ecosystems in the temperate regions? What environmental factors determine the geographic distribution of the different biome types (e.g., forest, grassland, and desert)?

Finally, at the biosphere level, the emphasis is on the linkages between ecosystems and other components of the earth system, such as the atmosphere. For example, how does the exchange of energy and materials between terrestrial ecosystems and the atmosphere influence regional and global climate patterns? Certain processes, such as movement of the element carbon between ecosystems and the atmosphere, operate at a global scale and require ecologists to collaborate with oceanographers, geologists, and atmospheric scientists.

Throughout our discussion, we have used this hierarchical view of nature and the unique set of patterns and process associated with each level—the individual population, community, ecosystem, landscape, biome, and biosphere—as an organizing framework for studying the science of ecology. In fact, the science of ecology is functionally organized into subdisciplines based on these different levels of organization, each using an array of specialized approaches and methodologies to address the unique set of questions that emerge at these different levels of ecological organization. The patterns and processes at these different levels of organization are linked, however, and identifying these linkages is our objective. For example, at the individual organism level, characteristics such as size, longevity, age at reproduction, and degree of parental care will directly influence rates of birth and survival for the collective of individuals comprising the species' population. At the community level, the same population will be influenced both positively and negatively through its interactions with populations of other species. In turn, the relative mix of species that make up the community will influence the collective properties of energy and nutrient exchange at the ecosystem level. As we shall see, patterns and processes at each level—from individuals to ecosystems—are intrinsically linked in a web of cause and effect with the patterns and processes operating at the other levels of this organizational hierarchy.

1.5 Ecologists Investigate Nature Using the Scientific Method

Although each level in the hierarchy of ecological systems has a unique set of questions on which ecologists focus their research, all ecological studies have one thing in common: they include the process known as the scientific method (**Figure 1.4**). This method demonstrates the power and limitations of science, and taken individually, each step of the scientific method involves commonplace procedures. Yet taken together, these procedures form a powerful tool for understanding nature.

All science begins with observation. In fact, this first step in the process defines the domain of science: if something cannot be observed, it cannot be investigated by science. The observation need not be direct, however. For example, scientists cannot directly observe the nucleus of an atom, yet its structure can be explored indirectly through a variety of methods. Secondly, the observation must be repeatable—able to be made by multiple observers. This constraint helps to minimize unsuspected bias, when an individual might observe what they *want* or think they *ought* to observe.

The second step in the scientific method is defining a problem—forming a question regarding the observation that has been made. For example, an ecologist working in the prairie grasslands of North America might observe that the growth and productivity (the rate at which plant biomass is being produced

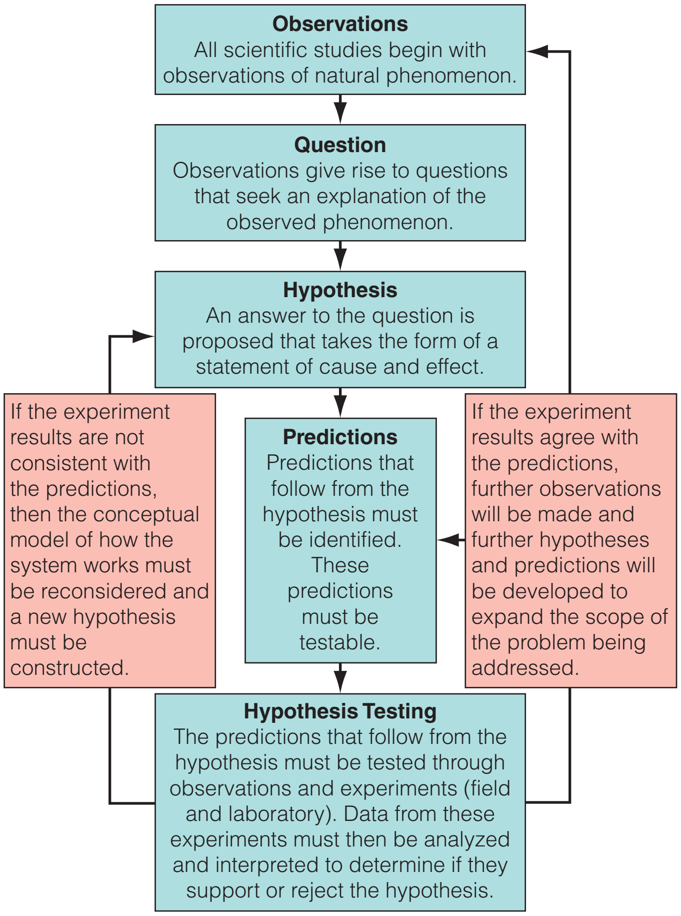


Figure 1.4 A simple representation of the scientific method.

per unit area per unit time: grams per meter squared per year [$g/m^2/yr$]) of grasses varies across the landscape. From this observation the ecologist may formulate the question, what environmental factors result in the observed variations in grassland productivity across the landscape? The question typically focuses on seeking an explanation for the observed patterns.

Once a question (problem) has been established, the next step is to develop a hypothesis. A **hypothesis** is an educated guess about what the answer to the question may be. The process of developing a hypothesis is guided by experience and knowledge, and it should be a statement of cause and effect that can be tested. For example, based on her knowledge that nitrogen availability varies across the different soil types found in the region and that nitrogen is an important nutrient limiting plant growth, the ecologist might hypothesize that *the observed variations in the growth and productivity of grasses across the prairie landscape are a result of differences in the availability of soil nitrogen*. As a statement of cause and effect, certain predictions follow from the hypothesis. If soil nitrogen is the factor limiting the growth and productivity of plants in the prairie grasslands, then grass productivity should be greater in areas with higher levels of soil nitrogen than in areas with lower levels of soil nitrogen. The next step is testing the hypothesis to see if the predictions that follow from the hypothesis do indeed hold true. This step requires gathering data (see **Quantifying Ecology 1.1**).

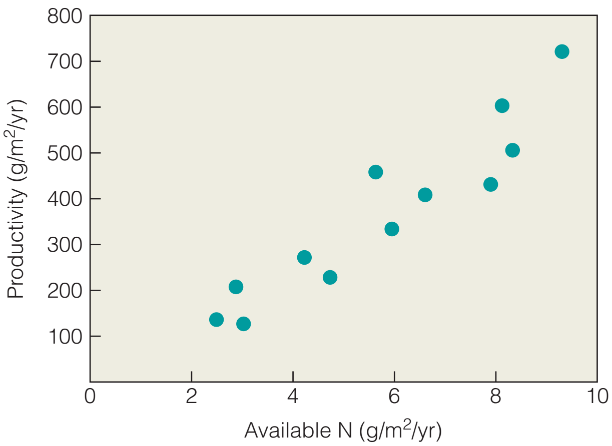


Figure 1.5 The response of grassland production to soil nitrogen availability. Nitrogen (N), the independent variable, is plotted on the *x*-axis; grassland productivity, the dependent variable, is plotted on the *y*-axis.

Interpreting Ecological Data

Q1. *In the above graph, which variable is the independent variable? Which is the dependent variable? Why?*

Q2. *Would you describe the relationship between available nitrogen and grassland productivity as positive or negative (inverse)?*

To test this hypothesis, the ecologist may gather data in several ways. The first approach might be a field study to examine how patterns of soil nitrogen and grass productivity covary (vary together) across the landscape. If nitrogen is controlling grassland productivity, productivity should increase with increasing soil nitrogen. The ecologist would measure nitrogen availability and grassland productivity at various sites across the landscape. Then, the relationship between these two variables, nitrogen and productivity, could be expressed graphically (see **Quantifying Ecology 1.2** on pages 24 and 25 to learn more about working with graphical data). Visit MasteringBiology at www.masteringbiology.com to work with histograms and scatter plots.

After you've become familiar with scatter plots, you'll see the graph of **Figure 1.5** shows nitrogen availability on the horizontal or *x*-axis and grassland productivity on the vertical or *y*-axis. This arrangement is important. The scientist is assuming that nitrogen is the cause and that grassland productivity is the effect. Because nitrogen (x) is the cause, we refer to it as the independent variable. Because it is hypothesized that grassland productivity (y) is influenced by the availability of nitrogen, we refer to it as the dependent variable. Visit MasteringBiology at www.masteringbiology.com for a tutorial on reading and interpreting graphs.

From the observations plotted in Figure 1.5, it is apparent that grassland productivity does, in fact, increase with increasing availability of nitrogen in the soil. Therefore, the data support the hypothesis. Had the data shown no relationship between grassland productivity and nitrogen, the ecologist would have rejected the hypothesis and sought a new explanation for the observed differences in grassland productivity across the landscape. However, although the data suggest that grassland