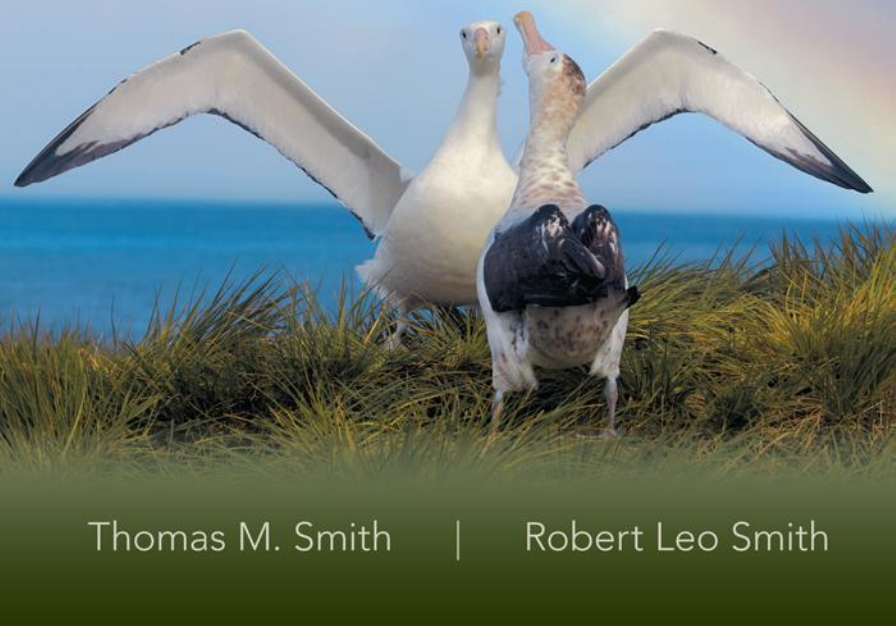
ELEMENTS OF Ecology

Ninth Edition



Thomas M. Smith | Robert Leo Smith

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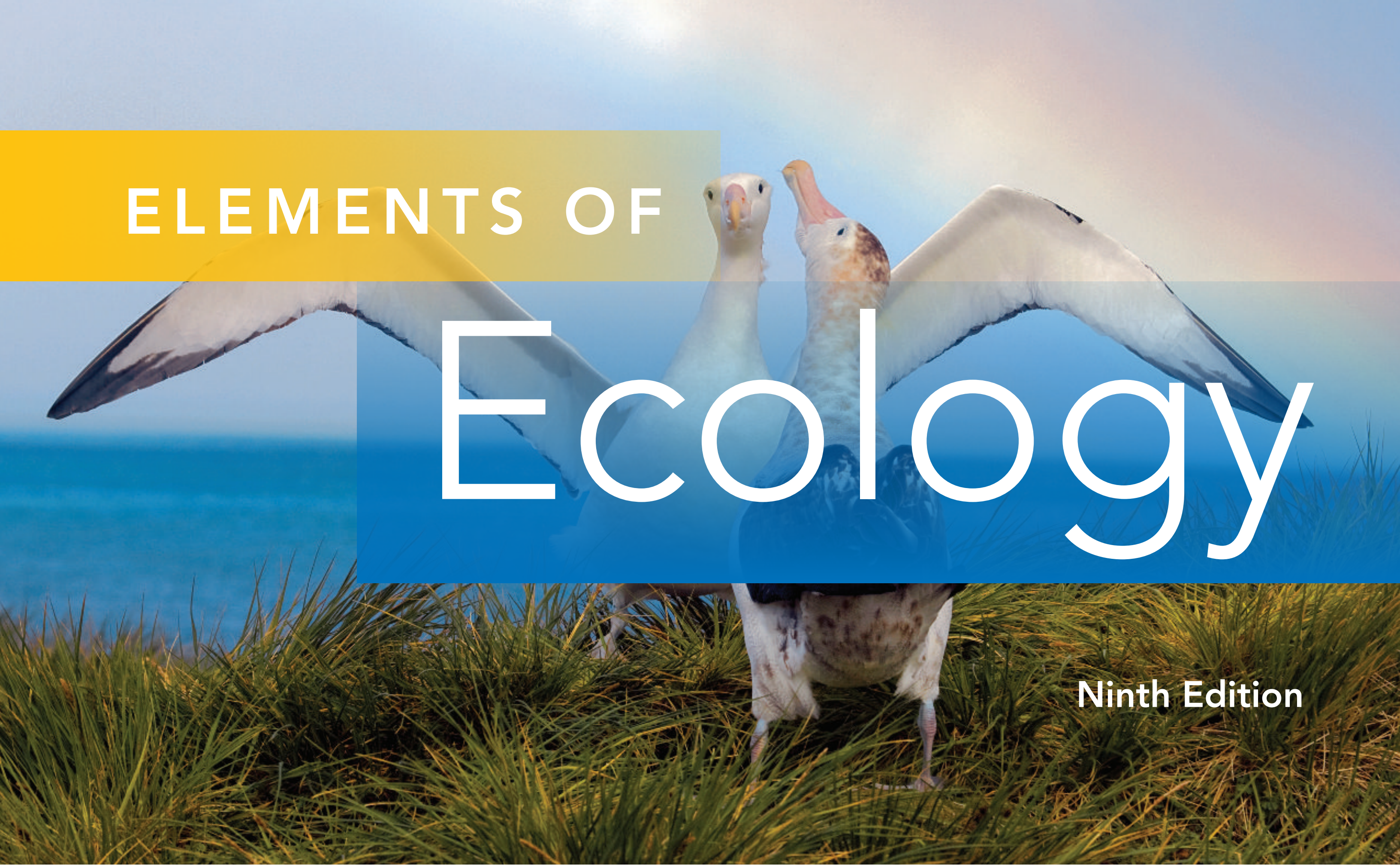

ELEMENTS OF Ecology

Ninth Edition

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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.

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Thomas M. Smith

Robert Leo Smith

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.

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

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.

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.

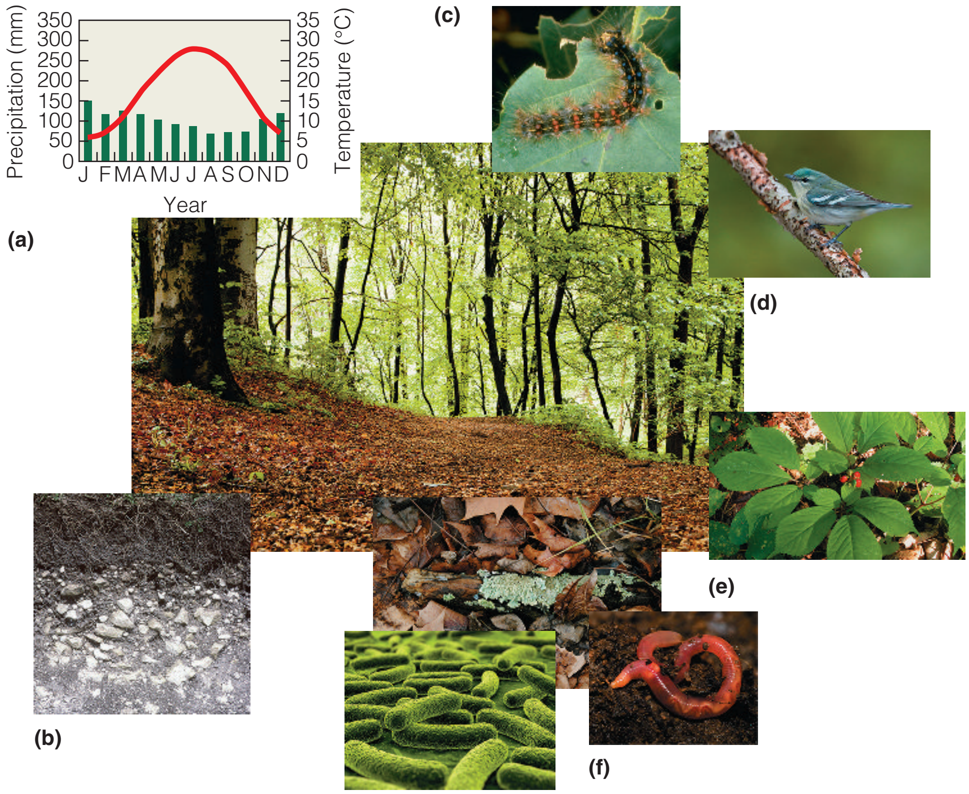

Figure 1.2 Example of the components and interactions that define a forest ecosystem. The abiotic components of the ecosystem, including the (a) climate and (b) soil, directly influence the forest trees. (c) Herbivores feed on the canopy, (d) while predators such as this warbler feed upon insects. (e) 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.

Individual

What characteristics allow the *Echinacea* to survive, grow, and reproduce in the environment of the prairie grasslands of central North America?

Population

Is the population of this species increasing, decreasing, or remaining relatively constant from year to year?

Community

How does this species interact with other species of plants and animals in the prairie community?

Ecosystem

How do yearly variations in rainfall influence the productivity of plants in this prairie grassland ecosystem?

Landscape

How do variations in topography and soils across the landscape influence patterns of species composition and diversity in the different prairie communities?

Biome

What features of geology and regional climate determine the transition from forest to prairie grassland ecosystems in North America?

Biosphere

What is the role of the grassland biome in the global carbon cycle?

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

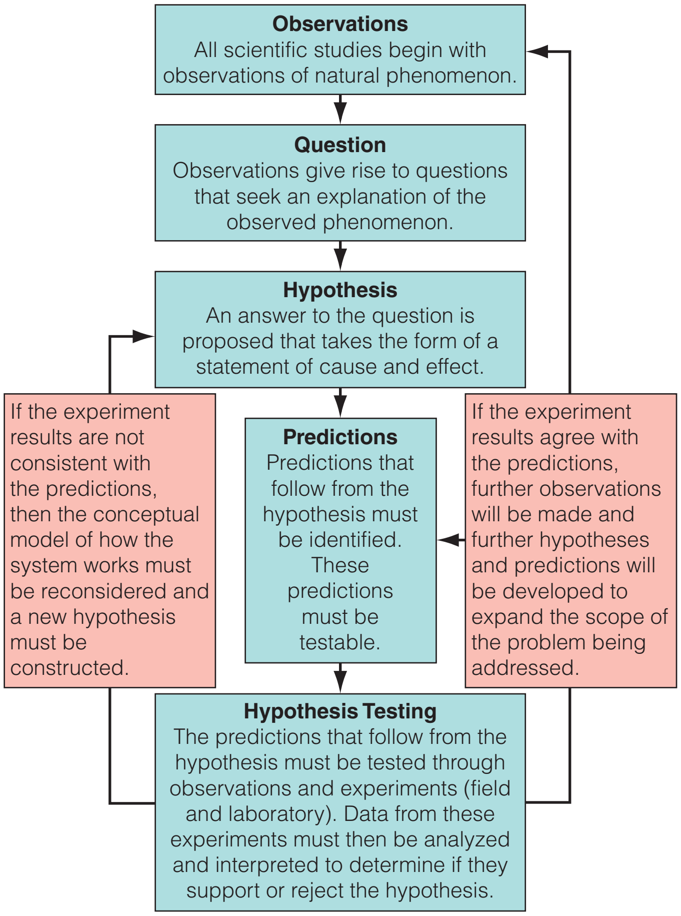

Figure 1.4 A simple representation of the scientific method.

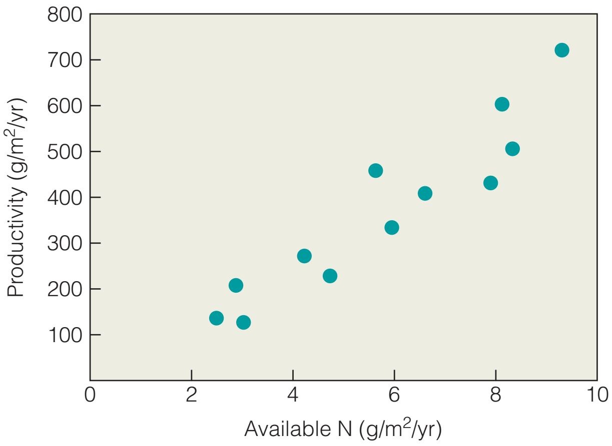

Figure 1.5 The response of grassland production to soil nitrogen availability. Nitrogen (N), the independent variable, is plotted on the *x*-axis; grassland productivity, the dependent variable, is plotted on the *y*-axis.

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)?*

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**).

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 8 and 9 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

QUANTIFYING ECOLOGY 1.1 Classifying Ecological Data

All ecological studies involve collecting data that includes observations and measurements for testing hypotheses and drawing conclusions about a population. The term *population* in this context refers to a **statistical population**. An investigator is highly unlikely to gather observations on *all* members of a total population, so the part of the population actually observed is referred to as a **sample**. From this sample data, the investigator will draw her conclusions about the population as a whole. However, not all data are of the same type; and the type of data collected in a study directly influences the mode of presentation, types of analyses that can be performed, and interpretations that can be made.

At the broadest level, data can be classified as either categorical or numerical. **Categorical data** are *qualitative*, that is, observations that fall into separate and distinct categories. The resulting data are labels or categories, such as the color of hair or feathers, sex, or reproductive status (pre-reproductive, reproductive, post-reproductive). Categorical data can be further subdivided into two categories: nominal and ordinal. **Nominal data** are categorical data in which objects fall into unordered categories, such as the previous examples of hair color or sex. In contrast, **ordinal data** are categorical data in which order is important, such as the example of reproductive status. In the special case where only two categories exist, such as in the case of presence or absence of a trait, categorical data are referred to as **binary.** Both nominal and ordinal data can be binary.

With **numerical data**, objects are "measured" based on some *quantitative* trait. The resulting data are a set of numbers, such as height, length, or weight. Numerical data can be subdivided into two categories: discrete and continuous. For **discrete data**, only certain values are possible, such as with integer values or counts. Examples include the number of offspring, number of seeds produced by a plant, or number of times a hummingbird visits a flower during the course of a day. With **continuous data**, any value within an interval theoretically is possible, limited only by the ability of the measurement device. Examples of this type of data include height, weight, or concentration.

1. What type of data does the variable "available N" (the *x*-axis) represent in Figure 1.5?
2. How might you transform this variable (available nitrogen) into categorical data? Would it be considered ordinal or nominal?

production does increase with increasing soil nitrogen, they do not prove that nitrogen is the *only* factor controlling grass growth and production. Some other factor that varies with nitrogen availability, such as soil moisture or acidity, may actually be responsible for the observed relationship. To test the hypothesis another way, the ecologist may choose to do an experiment. An experiment is a test under controlled conditions performed to examine the validity of a hypothesis. In designing the experiment, the scientist will try to isolate the presumed causal agent—in this case, nitrogen availability.

The scientist may decide to do a field experiment (**Figure 1.6**), adding nitrogen to some field sites and not to others. The investigator controls the independent variable (levels of nitrogen) in a predetermined way, to reflect observed variations in soil nitrogen availability across the landscape, and monitors the response of the dependent variable (plant growth). By observing the differences in productivity between the grasslands fertilized with nitrogen and those that were not, the investigator tries to test whether nitrogen is the causal agent. However, in choosing the experimental sites, the ecologist must try to locate areas where other factors that may influence productivity, such as moisture and acidity, are similar. Otherwise, she cannot be sure which factor is responsible for the observed differences in productivity among the sites.

Finally, the ecologist might try a third approach—a series of laboratory experiments (**Figure 1.7**). Laboratory experiments give the investigator much more control over the environmental conditions. For example, she can grow the native grasses in the greenhouse under conditions of controlled temperature, soil acidity, and water availability. If the plants exhibit increased growth with higher nitrogen fertilization, the investigator has further evidence in support of the hypothesis. Nevertheless, she faces a limitation common to all laboratory experiments; that is, the results are not directly applicable in the field. The response of grass plants under controlled laboratory conditions may not be the same as their response under natural conditions in the field. There, the plants are part of the ecosystem and interact with other plants, animals, and the

Figure 1.6 Field experiment at the Cedar Creek Long Term Ecological Research (LTER) site in central Minnesota, operated by the University of Minnesota. Experimental plots such as these are used to examine the effects of elevated nitrogen deposition, increased concentrations of atmospheric carbon dioxide, and loss of biodiversity on ecosystem functioning.

QUANTIFYING ECOLOGY 1.2 Displaying Ecological Data: Histograms and Scatter Plots

Whichever type of data an observer collects (see Quantifying Ecology 1.1), the process of interpretation typically begins with a graphical display of observations. The most common method of displaying a single data set is constructing a **frequency distribution**. A frequency distribution is a count of the number of observations (frequency) having a given score or value. For example, consider this set of observations regarding flower color in a sample of 100 pea plants:

Flower color	Purple	Pink	White
Frequency	50	35	15

These data are categorical and nominal since the categories have no inherent order.

Frequency distributions are likewise used to display continuous data. This set of continuous data represents body lengths (in centimeters) of 20 sunfish sampled from a pond:

8.83, 9.25, 8.77, 10.38, 9.31, 8.92, 10.22, 7.95, 9.74, 9.51, 9.66, 10.42, 10.35, 8.82, 9.45, 7.84, 11.24, 11.06, 9.84, 10.75

With continuous data, the frequency of each value is often a single instance because multiple data points are unlikely to be exactly the same. Therefore, continuous data are normally grouped into discrete categories, with each category representing a defined range of values. Each category must not overlap; each observation must belong to only one category. For example, the body length data could be grouped into discrete categories:

Body length (intervals, cm)	Number of individuals
7.00–7.99	2
8.00–8.99	4
9.00–9.99	7
10.00–10.99	5
11.00–11.99	2

Once the observations have been grouped into categories, the resulting frequency distribution can then be displayed as a **histogram** (type of bar graph; **Figure 1a**). The *x*-axis represents the discrete intervals of body length, and the *y*-axis represents the number of individuals whose body length falls within each given interval.

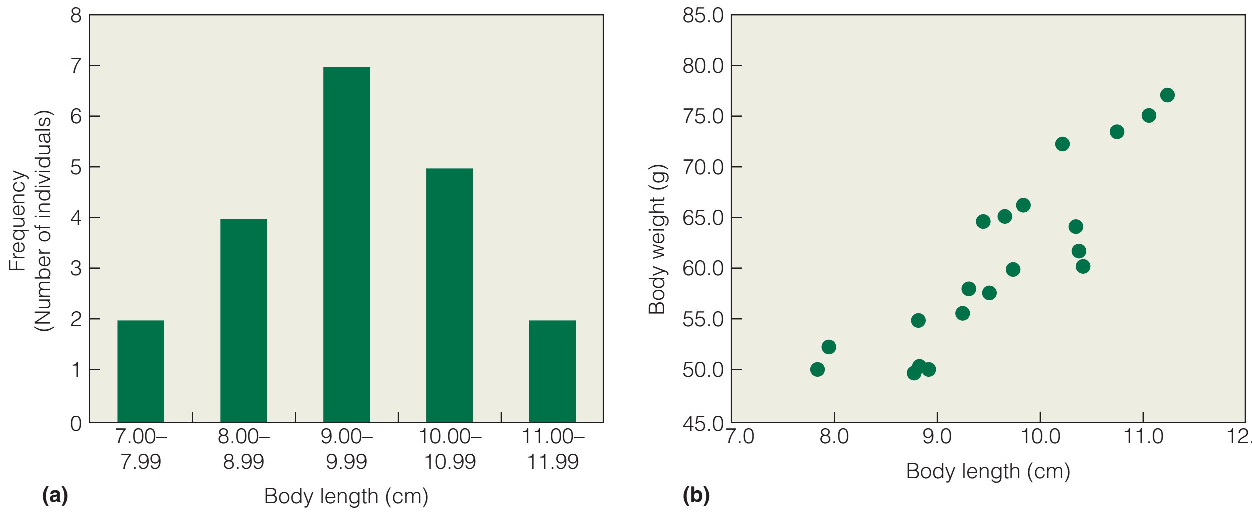

Figure 1 (a) An example of a histogram relating the number of individuals belonging to different categories of body length from a sample of the sunfish population. (b) Scatter plot relating body length (*x*-axis) and body weight (*y*-axis) for the sample of sunfish presented in (a).

physical environment. Despite this limitation, the ecologist has accumulated additional data describing the basic growth response of the plants to nitrogen availability.

Having conducted several experiments that confirm the link between patterns of grass productivity to nitrogen availability, the ecologist may now wish to explore this relationship further, to see how the relationship between productivity and nitrogen is influenced by other environmental factors that vary across the prairie landscape. For example, how do differences in rainfall and soil moisture across the region influence the relationship between grass production and soil nitrogen? Once again hypotheses are developed, predictions made, and experiments conducted. As the ecologist develops a more detailed understanding of how various environmental factors interact with

In effect, the continuous data are transformed into categorical data for the purposes of graphical display. Unless there are previous reasons for defining categories, defining intervals is part of the data interpretation process and the search for patterns. For example, how would the pattern represented by the histogram in Figure 1a differ if the intervals were in units of 1 but started with 7.50 (7.50–8.49, 8.50–9.49, etc.)?

Often, however, the researcher is examining the relationship between two variables or sets of observations. When both variables are numerical, the most common method of graphically displaying the data is by using a scatter plot. A **scatter plot** is constructed by defining two axes (*x* and *y*), each representing one of the two variables being examined. For example, suppose the researcher who collected the observations of body length for sunfish netted from the pond also measured their weight in grams. The investigator might be interested in whether there is a relationship between body length and weight in sunfish.

In this example, body length would be the *x*-axis, or independent variable (Section 1.5), and body weight would be the *y*-axis, or dependent variable. Once the two axes are defined, each individual (sunfish) can be plotted as a point on the graph, with the position of the point being defined by its respective values of body length and weight (**Figure 1b**).

Scatter plots can be described as belonging to one of three general patterns, as shown in **Figure 2**. In plot (a) there is a general trend for *y* to increase with increasing values of *x*. In this case the relationship between *x* and *y* is said to be positive (as with the example of body length and weight for sunfish). In plot (b) the pattern is reversed, and *y* decreases with increasing values of *x*. In this case the relationship between *x* and *y* is said to be negative, or inverse. In plot (c) there is no apparent relationship between *x* and *y*.

You will find many types of graphs throughout our discussion but most will be histograms and scatter plots. No matter which type of graph is presented, ask yourself the same set of questions—listed below—to help interpret the results. Review this set of questions by applying them to the graphs in Figure 1. What do you find out?

1. What type of data do the observations represent?
2. What variables do each of the axes represent, and what are their units (cm, g, color, etc.)?
3. How do values of *y* (the dependent variable) vary with values of *x* (the independent variable)?

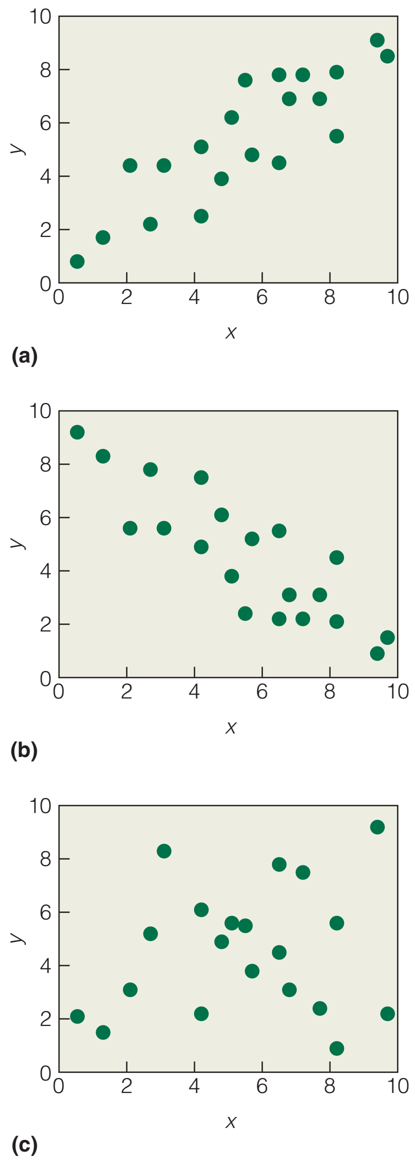

Figure 2 Three general patterns for scatter plots.

Go to Analyzing Ecological Data at www.masteringbiology.com to further explore how to display data graphically.

soil nitrogen to control grass production, a more general theory of the influence of environmental factors controlling grass production in the grassland prairies may emerge. A **theory** is an integrated set of hypotheses that together explain a broader set of observations than any single hypothesis—such as a general theory of environmental controls on productivity of the prairie grassland ecosystems of North America.

Although the diagram of the scientific method presented in Figure 1.4 represents the process of scientific investigation as a sequence of well-defined steps that proceeds in a linear fashion, in reality, the process of scientific research often proceeds in a nonlinear fashion. Scientists often begin an investigation based on readings of previously published studies, discussions with colleagues, or informal observations made in

(a) (b)

Figure 1.7 (a) Undergraduate research students at Harvard Forest erect temporary greenhouses that were used to create different carbon dioxide (CO_2) treatments for a series of experiments directed at testing the response of ragweed (*Ambrosia artemisiifolia*) to elevated atmospheric CO_2. (b) Response to elevated CO_2 was determined by measuring the growth, morphology, and reproductive characteristics of individual plants from different populations.

the field or laboratory rather than any formal process. Often during hypothesis testing, observations may lead the researcher to modify the experimental design or redefine the original hypothesis. In reality, the practice of science involves unexpected twist and turns. In some cases, unexpected observations or results during the initial investigation may completely change the scope of the study, leading the researcher in directions never anticipated. Whatever twists and unanticipated turns may occur, however, the process of science is defined by the fundamental structure and constraints of the scientific method.

1.6 Models Provide a Basis for Predictions

Scientists use the understanding derived from observation and experiments to develop models. Data are limited to the special case of what happened when the measurements were made. Like photographs, data represent a given place and time. Models use the understanding gained from the data to predict what will happen in some other place and time.

Models are abstract, simplified representations of real systems. They allow us to predict some behavior or response using a set of explicit assumptions, and as with hypotheses, these predictions should be testable through further observation or experiments. Models may be mathematical, like computer simulations, or they may be verbally descriptive, like Darwin's theory of evolution by natural selection (see Chapter 5). Hypotheses are models, although the term *model* is typically reserved for circumstances in which the hypothesis has at least some limited support through observations and experimental results. For example, the hypothesis relating grass production to nitrogen availability is a model. It predicts that plant productivity will increase with increasing nitrogen availability. However, this prediction is qualitative—it does not predict *how much* plant productivity will increase. In contrast, mathematical models usually offer quantitative predictions. For example, from the data in Figure 1.5, we can develop a regression equation—a form of statistical model—to predict the amount of grassland productivity per unit of nitrogen in the soil (**Figure 1.8**). Visit MasteringBiology at www.masteringbiology.com to review regression analysis.

All of the approaches just discussed—observation, experimentation, hypothesis testing, and development of models—appear throughout our discussion to illustrate basic concepts and relationships. They are the basic tools of science. For every topic, an array of figures and tables present the observations, experimental data, and model predictions used to test specific hypotheses regarding pattern and process at the different levels of ecological organization. Being able to analyze and interpret the data presented in these figures and tables is essential to your understanding of the science of ecology. To help you develop these skills, we have annotated certain figures and tables to guide you in their interpretation. In other cases, we pose questions that ask you to interpret, analyze, and draw conclusions from the data presented. These figures and tables are labeled *Interpreting Ecological Data*. (See Figure 2.15 on page 23 for the first example.)

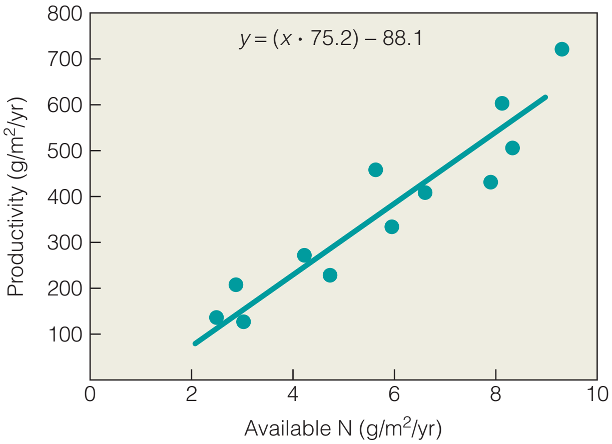

Figure 1.8 A simple linear regression model to predict grassland productivity (*y*-axis) from nitrogen availability (*x*-axis). The general form of the equation is $y = (x \times b) + a$, where b is the slope of the line (75.2) and a is the *y*-intercept (–88.1), or the value of y where the line intersects the *y*-axis (when $x = 0$).

Interpreting Ecological Data

Q1. *How could you use the simple linear regression model presented to predict productivity for a grassland site not included in the graph?*

Q2. *What is the predicted productivity for a site with available nitrogen of 5 g/m^2/yr? (Use the linear regression equation.)*

1.7 Uncertainty Is an Inherent Feature of Science

Collecting observations, developing and testing hypotheses, and constructing predictive models all form the backbone of the scientific method (see Figure 1.4). It is a continuous process of testing and correcting concepts to arrive at explanations for the variation we observe in the world around us, thus unifying observations that on first inspection seem unconnected. The difference between science and art is that, although both pursuits involve creation of concepts, in science, the exploration of concepts is limited to the facts. In science, the only valid means of judging a concept is by testing its empirical truth.

However, scientific concepts have no permanence because they are only our interpretations of natural phenomena. We are limited to inspecting only a part of nature because to understand, we have to simplify. As discussed in Section 1.5, in designing experiments, we control the pertinent factors and try to eliminate others that may confuse the results. Our intent is to focus on a subset of nature from which we can establish cause and effect. The trade-off is that whatever cause and effect we succeed in identifying represents only a partial connection to the nature we hope to understand. For that reason, when experiments and observations support our hypotheses, and when the predictions of the models are verified, our job is still not complete. We work to loosen the constraints imposed by the need to simplify so that we can understand. We expand our hypothesis to cover a broader range of conditions and once again begin testing its ability to explain our new observations.

It may sound odd at first, but science is a search for evidence that proves our concepts wrong. Rarely is there only one possible explanation for an observation. As a result, any number of hypotheses may be developed that might be consistent with an observation. The determination that experimental data are consistent with a hypothesis does not prove that the hypothesis is true. The real goal of hypothesis testing is to eliminate incorrect ideas. Thus, we must follow a process of elimination, searching for evidence that proves a hypothesis wrong. Science is essentially a self-correcting activity, dependent on the continuous process of debate. Dissent is the activity of science, fueled by free inquiry and independence of thought. To the outside observer, this essential process of debate may appear to be a shortcoming. After all, we depend on science for the development of technology and the ability to solve problems. For the world's current environmental issues, the solutions may well involve difficult ethical, social, and economic decisions. In this case, the uncertainty inherent in science is discomforting. However, we must not mistake uncertainty for confusion, nor should we allow disagreement among scientists to become an excuse for inaction. Instead, we need to understand the uncertainty so that we may balance it against the costs of inaction.

1.8 Ecology Has Strong Ties to Other Disciplines

The complex interactions taking place within ecological systems involve all kinds of physical, chemical, and biological processes. To study these interactions, ecologists must draw on other sciences. This dependence makes ecology an interdisciplinary science.

Although we explore topics that are typically the subject of disciplines such as biochemistry, physiology, and genetics, we do so only in the context of understanding the interplay of organisms with their environment. The study of how plants take up carbon dioxide and lose water, for example, belongs to plant physiology (see Chapter 6). Ecology looks at how these processes respond to variations in rainfall and temperature. This information is crucial to understanding the distribution and abundance of plant populations and the structure and function of ecosystems on land. Likewise, we must draw on many of the physical sciences, such as geology, hydrology, and meteorology. They help us chart other ways in which organisms and environments interact. For instance, as plants take up water, they influence soil moisture and the patterns of surface water flow. As they lose water to the atmosphere, they increase atmospheric water content and influence regional patterns of precipitation. The geology of an area influences the availability of nutrients and water for plant growth. In each example, other scientific disciplines are crucial to understanding how individual organisms both respond to and shape their environment.

In the 21st century, ecology is entering a new frontier, one that requires expanding our view of ecology to include the dominant role of humans in nature. Among the many environmental problems facing humanity, four broad and interrelated areas are crucial: human population growth, biological diversity, sustainability, and global climate change. As the human population increased from approximately 500 million to more than 7 billion in the past two centuries, dramatic changes in land use have altered Earth's surface. The clearing of forests for agriculture has destroyed many natural habitats, resulting in a rate of species extinction that is unprecedented in Earth's history. In addition, the expanding human population is exploiting natural resources at unsustainable levels. As a result of the growing demand for energy from fossil fuels that is needed to sustain economic growth, the chemistry of the atmosphere is changing in ways that are altering Earth's climate. These environmental problems are ecological in nature, and the science of ecology is essential to understanding their causes and identifying ways to mitigate their impacts. Addressing these issues, however, requires a broader interdisciplinary framework to better understand their historical, social, legal, political, and ethical dimensions. That broader framework is known as **environmental science**. Environmental science examines the impact of humans on the natural environment and as such covers a wide range of topics including agronomy, soils, demography, agriculture, energy, and hydrology, to name but a few.

Throughout the text, we use the *Ecological Issues & Applications* sections of each chapter to highlight topics relating to current environmental issues regarding human impacts on the environment and to illustrate the importance of the science of ecology to better understanding the human relationship with the environment.

1.9 The Individual Is the Basic Unit of Ecology

As we noted previously, ecology encompasses a broad area of investigation—from the individual organism to the biosphere. Our study of the science of ecology uses this hierarchical framework in the chapters that follow. We begin with the individual organism, examining the processes it uses and constraints it faces in maintaining life under varying environmental conditions. The individual organism forms the basic unit in ecology. The individual senses and responds to the prevailing physical environment. The collective properties of individual births and deaths drive the dynamics of populations, and individuals of different species interact with one another in the context of the community. But perhaps most importantly, the individual, through the process of reproduction, passes genetic information to successive individuals, defining the nature of individuals that will compose future populations, communities, and ecosystems. At the individual level we can begin to understand the mechanisms that give rise to the diversity of life and ecosystems on Earth—mechanisms that are governed by the process of natural selection. But before embarking on our study of ecological systems, we examine characteristics of the abiotic (physical and chemical) environment that function to sustain and constrain the patterns of life on our planet.

ECOLOGICAL Issues & Applications

Ecology Has a Rich History

The genealogy of most sciences is direct. Tracing the roots of chemistry and physics is relatively easy. The science of ecology is different. Its roots are complex and intertwined with a wide array of scientific advances that have occurred in other disciplines within the biological and physical sciences. Although the term *ecology* did not appear until the mid-19th century and took another century to enter the vernacular, the idea of ecology is much older.

Arguably, ecology goes back to the ancient Greek scholar Theophrastus, a friend of Aristotle, who wrote about the relations between organisms and the environment. On the other hand, ecology as we know it today has vital roots in plant geography and natural history.

In the 1800s, botanists began exploring and mapping the world's vegetation. One of the early plant geographers was Carl Ludwig Willdenow (1765–1812). He pointed out that similar climates supported vegetation similar in form, even though the species were different. Another was Friedrich Heinrich Alexander von Humboldt (1769–1859), for whom the Humboldt Current, flowing along the west coast of South America, is named. He spent five years exploring Latin America, including the Orinoco and Amazon rivers. Humboldt correlated vegetation with environmental characteristics and coined the term *plant association*. The recognition that the form and function of plants within a region reflects the constraints imposed by the physical environment led the way for a new generation of scientists that explored the relationship between plant biology and plant geography (see Chapter 23).

Among this new generation of plant geographers was Johannes Warming (1841–1924) at the University of Copenhagen, who studied the tropical vegetation of Brazil. He wrote the first text on plant ecology, *Plantesamfund*. Warming integrated plant morphology, physiology, taxonomy, and biogeography into a coherent whole. This book had a tremendous influence on the development of ecology.

Meanwhile, activities in other areas of natural history also assumed important roles. One was the voyage of Charles Darwin (1809–1882) on the *Beagle*. Working for years on notes and collections from this trip, Darwin compared similarities and dissimilarities among organisms within and among continents. He attributed differences to geological barriers. He noted how successive groups of plants and animals, distinct yet obviously related, replaced one another.

Developing his theory of evolution and the origin of species, Darwin came across the writings of Thomas Malthus (1766–1834). An economist, Malthus advanced the principle that populations grow in a geometric fashion, doubling at regular intervals until they outstrip the food supply. Ultimately, a "strong, constantly operating force such as sickness and premature death" would restrain the population. From this concept Darwin developed the idea of "natural selection" as the mechanism guiding the evolution of species (see Chapter 5).

Meanwhile, unbeknownst to Darwin, an Austrian monk, Gregor Mendel (1822–1884), was studying the transmission of characteristics from one generation of pea plants to another in his garden. Mendel's work on inheritance and Darwin's work on natural selection provided the foundation for the study of evolution and adaptation, the field of **population genetics**.

Darwin's theory of natural selection, combined with the new understanding of genetics (the means by which characteristics are transmitted from one generation to the next) provided the mechanism for understanding the link between organisms and their environment, which is the focus of ecology.

Early ecologists, particularly plant ecologists, were concerned with observing the patterns of organisms in nature, and attempting to understand how patterns were formed and maintained by interactions with the physical environment. Some, notably Frederic E. Clements (**Figure 1.9**), sought some system of organizing nature. He proposed that the plant community behaves as a complex organism or *superorganism*

Figure 1.9 The ecologist Frederic E. Clements in the field collecting data.

that grows and develops through stages to a mature or climax state (see Chapter 16). His idea was accepted and advanced by many ecologists. A few ecologists, however, notably Arthur G. Tansley, did not share this view. In its place Tansley advanced a holistic and integrated ecological concept that combined living organisms and their physical environment into a system, which he called the ecosystem (see Chapter 20).

Whereas the early plant ecologists were concerned mostly with terrestrial vegetation, another group of European biologists was interested in the relationship between aquatic plants and animals and their environment. They advanced the ideas of organic nutrient cycling and feeding levels, using the terms *producers* and *consumers*. Their work influenced a young limnologist at the University of Minnesota, R. A. Lindeman. He traced "energy-available" relationships within a lake community. His 1942 paper, "The Trophic-Dynamic Aspects of Ecology," marked the beginning of **ecosystem ecology**, the study of whole living systems.

Lindeman's theory stimulated further pioneering work in the area of energy flow and nutrient cycling by G. E. Hutchinson of Yale University (**Figure 1.10**) and E. P. and H. T. Odum of the University of Georgia. Their work became a foundation of ecosystem ecology. The use of radioactive tracers, a product of the atomic age, to measure the movements of energy and nutrients through ecosystems and the use of computers to analyze large amounts of data stimulated the development of **systems ecology**, the application of general system theory and methods to ecology.

Animal ecology initially developed largely independently of the early developments in plant ecology. The beginnings of animal ecology can be traced to two Europeans, R. Hesse of Germany and Charles Elton of England. Elton's *Animal Ecology* (1927) and Hesse's *Tiergeographie auf logischer grundlage* (1924), translated into English as *Ecological Animal Geography*, strongly influenced the development of animal ecology in the United States. Charles Adams and Victor Shelford were two pioneering U.S. animal ecologists. Adams published the first textbook on animal ecology, *A Guide to the Study of Animal Ecology* (1913). Shelford wrote *Animal Communities in Temperate America* (1913).

Figure 1.10 Ecologist G. Evelyn Hutchinson in his lab at Yale University.

Shelford gave a new direction to ecology by stressing the interrelationship between plants and animals. Ecology became a science of communities. Some previous European ecologists, particularly the marine biologist Karl Mobius, had developed the general concept of the community. In his essay "An Oyster Bank is a Biocenose" (1877), Mobius explained that the oyster bank, although dominated by one animal, was really a complex community of many interdependent organisms. He proposed the word *biocenose* for such a community. The word comes from the Greek, meaning *life having something in common*.

The appearance in 1949 of the encyclopedic *Principles of Animal Ecology* by five second-generation ecologists from the University of Chicago (W. C. Allee, A. E. Emerson, Thomas Park, Orlando Park, and K. P. Schmidt) pointed to the direction that modern ecology would take. It emphasized feeding relationships and energy budgets, population dynamics, and natural selection and evolution.

During the period of development of the field of animal ecology, natural history observations also focused on the behavior of animals. This focus on animal behavior began with 19th-century behavioral studies including those of ants by William Wheeler and of South American monkeys by Charles Carpenter. Later, the pioneering studies of Konrad Lorenz and Niko Tinbergen on the role of imprinting and instinct in the social life of animals, particularly birds and fish, gave rise to **ethology**. It spawned an offshoot, **behavioral ecology**, exemplified by L. E. Howard's early study on territoriality in birds. Behavioral ecology is concerned with intraspecific and interspecific relationships such as mating, foraging, defense, and how behavior is influenced by natural selection.

The writings of the economist Malthus that were so influential in the development of Darwin's ideas regarding the origin of species also stimulated the study of natural populations. The study of populations in the early 20th century branched into two fields. One, **population ecology**, is concerned with population growth (including birthrates and death rates), regulation and intraspecific and interspecific competition, mutualism, and predation. The other, a combination of population genetics and population ecology is **evolutionary ecology**, which deals with the role of natural selection in physical and behavioral adaptations and speciation. Focusing on adaptations, **physiological ecology** is concerned with the responses of individual organisms to temperature, moisture, light, and other environmental conditions.

Closely associated with population and evolutionary ecology is **community ecology**, with its focus on species interactions. One of the major objectives of community ecology is to understand the origin, maintenance, and consequences of species diversity within ecological communities.

With advances in biology, physics, and chemistry throughout the latter part of the 20th century, new areas of study in ecology emerged. The development of aerial photography and later the launching of satellites by the U.S. space program provided scientists with a new perspective of the surface of Earth through the use of remote sensing data. Ecologists began to explore spatial processes that linked adjacent communities and ecosystems through the new emerging field of **landscape ecology**. A new appreciation of the impact of changing land use on natural ecosystems led to the development of **conservation ecology**, which applies principles from different fields, from ecology to economics and sociology, to the maintenance of biological diversity. The application of principles of ecosystem development and function to the restoration and management of disturbed lands gave rise to **restoration ecology**, whereas understanding Earth as a system is the focus of the newest area of ecological study, **global ecology**.

Ecology has so many roots that it probably will always remain multifaceted—as the ecological historian Robert McIntosh calls it, "a polymorphic discipline." Insights from these many specialized areas of ecology will continue to enrich the science as it moves forward in the 21st century.

SUMMARY

Ecology 1.1

Ecology is the scientific study of the relationships between organisms and their environment. The environment includes the physical and chemical conditions and 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.

Ecosystems 1.2

Organisms interact with their environment in the context of the ecosystem. Broadly, the ecosystem consists of two components, the living (biotic) and the physical (abiotic), interacting as a system.

Hierarchical Structure 1.3

Ecological systems may be viewed in a hierarchical framework, from individual organisms to the biosphere. Organisms of the same species that inhabit a given physical environment make up a population. Populations of different kinds of organisms interact with members of their own species as well as with individuals of other species. These interactions range from competition for shared resources to interactions that are mutually beneficial for the individuals of both species involved. Interacting populations make up a biotic community. The community plus the physical environment make up an ecosystem.

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. Geographic regions having similar geological and climatic conditions support similar types of communities and ecosystems, referred to as biomes. The highest level of organization of ecological systems is the biosphere—the thin layer around Earth that supports all of life.

Ecological Studies 1.4

At each level in the hierarchy of ecological systems—from the individual organism to the biosphere—a different and unique set of patterns and processes emerges; subsequently, a different set of questions and approaches for studying these patterns and processes is required.

Scientific Method 1.5

All ecological studies are conducted by using the scientific method. All science begins with observation, from which questions emerge. The next step is the development of a hypothesis—a proposed answer to the question. The hypothesis must be testable through observation and experiments.

Models 1.6

From research data, ecologists develop models. Models allow us to predict some behavior or response using a set of explicit assumptions. They are abstractions and simplifications of natural phenomena. Such simplification is necessary to understand natural processes.

Uncertainty in Science 1.7

An inherent feature of scientific study is uncertainty; it arises from the limitation posed by focusing on only a small subset of nature, and it results in an incomplete perspective. Because we can develop any number of hypotheses that may be consistent with an observation, determining that experimental data are consistent with a hypothesis is not sufficient to prove that the hypothesis is true. The real goal of hypothesis testing is to eliminate incorrect ideas.

An Interdisciplinary Science 1.8

Ecology is an interdisciplinary science because the interactions of organisms with their environment and with one another involve physiological, behavioral, and physical responses. The study of these responses draws on such fields as physiology, biochemistry, genetics, geology, hydrology, and meteorology.

Individuals 1.9

The individual organism forms the basic unit in ecology. It is the individual that responds to the environment and passes genes to successive generations. It is the collective birth and death of individuals that determines the dynamics of populations, and the interactions among individuals of the same and different species that structures communities.

History Ecological Issues & Applications

Ecology has its origin in natural history and plant geography. Over the past century it has developed into a science that has its roots in disciplines as diverse as genetics and systems engineering.

STUDY QUESTIONS

1. How do ecology and environmentalism differ? In what way does environmentalism depend on the science of ecology?
2. Define the terms *population*, *community*, *ecosystem*, *landscape*, *biome*, and *biosphere*.
3. How might including the abiotic environment within the framework of the ecosystem help ecologists achieve the basic goal of understanding the interaction of organisms with their environment?
4. What is a hypothesis? What is the role of hypotheses in science?
5. An ecologist observes that the diet of a bird species consists primarily of large grass seeds (as opposed to smaller grass seeds or the seeds of other herbaceous plants found in the area). He hypothesizes that the birds are choosing the larger seeds because they have a higher concentration of nitrogen than do other types of seeds at the site. To test the hypothesis, the ecologist compares the large grass seeds with the other types of seeds, and the results clearly show that the large grass seeds do indeed have a much higher concentration of nitrogen. Did the ecologist prove the hypothesis to be true? Can he conclude that the birds select the larger grass seeds because of their higher concentration of nitrogen? Why or why not?
6. What is a model? What is the relationship between hypotheses and models?
7. Given the importance of ecological research in making political and economic decisions regarding current environmental issues such as global warming, how do you think scientists should communicate uncertainties in their results to policy makers and the public?

FURTHER READINGS

Classic Studies

Bates, M. 1956. *The nature of natural history*. New York: Random House.

A lone voice in 1956, Bates shows us that environmental concerns have a long history prior to the emergence of the modern environmental movement. A classic that should be read by anyone interested in current environmental issues.

McKibben, W. 1989. *The end of nature*. New York: Random House.

In this provocative book, McKibben explores the philosophies and technologies that have brought humans to their current relationship with the natural world.

McIntosh, R. P. 1985. *The background of ecology: Concept and theory*. Cambridge: Cambridge University Press.

McIntosh provides an excellent history of the science of ecology from a scientific perspective.

Current Research

Coleman, D. 2010. *Big ecology; the emergence of ecosystem science*. Berkeley, University of California Press.

History of the development of large-scale ecosystem research and its politics and personalities as told by one of the participants.

Edgerton, F. N. 2012. *Roots of ecology*. Berkeley: University of California Press.

This book explores the deep ancestry of the science of ecology from the early ideas of Herodotos, Plato, and Pliny, up through those of Linnaeus, Darwin, and Haeckel.

Golley, F. B. 1993. *A history of the ecosystem concept in ecology: More than the sum of its parts*. New Haven: Yale University Press.

Covers the evolution and growth of the ecosystem concept as told by someone who was a major contributor to ecosystem ecology.

Kingsland, S. E. 2005. *The evolution of American ecology, 1890–2000*. Baltimore: Johns Hopkins University Press.

A sweeping, readable review of the evolution of ecology as a discipline in the United States, from its botanical beginnings to ecosystem ecology as colored by social, economic, and scientific influences.

Savill, P. S., C. M. Perrins, K. J. Kirby, N. Fisher, eds. 2010. *Wytham Woods: Oxford's ecological laboratory*. Oxford: Oxford University Press.

A revealing insight into some of the most significant population ecology studies by notable pioneering population ecologists such as Elton, Lack, Ford, and Southwood.

Worster, D. 1994. *Nature's economy*. Cambridge: Cambridge University Press.

This history of ecology is written from the perspective of a leading figure in environmental history.

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CHAPTER 2

Climate

As the sun rises, warming the morning air in this tropical rain forest on the island of Borneo, fog that has formed in the cooler night air begins to evaporate.

CHAPTER GUIDE

WHAT DETERMINES WHETHER a particular geographic region will be a tropical forest, a grassy plain, or a barren landscape of sand dunes? The aspect of the physical environment that most influences a particular ecosystem by placing the greatest constraint on organisms is climate. *Climate* is a term we tend to use loosely. In fact, people sometimes confuse climate with weather. **Weather** is the combination of temperature, humidity, precipitation, wind, cloudiness, and other atmospheric conditions occurring at a specific place and time. **Climate** is the long-term average pattern of weather and may be local, regional, or global.

The structure of terrestrial ecosystems is largely defined by the dominant plants, which in turn reflect the prevailing physical environmental conditions, namely climate (see Chapter 23). Geographic variations in climate, primarily temperature and precipitation, govern the large-scale distribution of plants and therefore the nature of terrestrial ecosystems. Here, we learn how climate determines the availability of thermal energy and water on Earth's surface and influences the amount of solar energy that plants may harness.

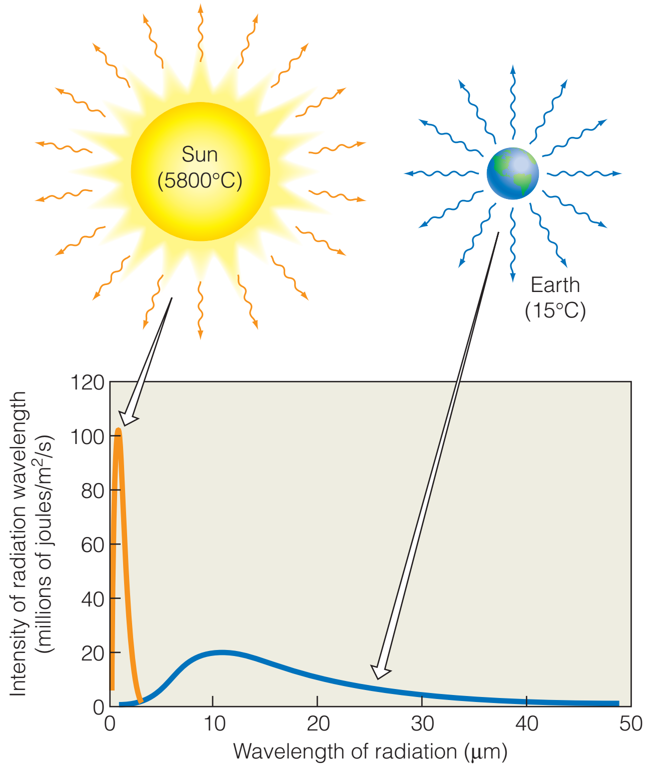


Figure 2.2 The wavelength of radiation emitted by an object is a function of its temperature. The Sun, with an average surface temperature of 5800°C, emits shortwave radiation as compared to Earth, with an average surface temperature of 15°C, which emits longwave radiation.

2.1 Surface Temperatures Reflect the Difference between Incoming and Outgoing Radiation

Solar radiation—the electromagnetic energy (**Figure 2.1**) emanating from the Sun—travels more or less unimpeded through the vacuum of space until it reaches Earth's atmosphere. Scientists conceptualize solar radiation as a stream of photons, or packets of energy, that—in one of the great paradoxes of science—behave either as waves or as particles, depending on how they are observed. Scientists characterize waves of energy in terms of their wavelength (λ), or the physical distances between successive crests, and their frequency (ν), or the number of crests that pass a given point per second. All objects emit radiant energy, typically across a wide range of wavelengths. The exact nature of the energy emitted, however, depends on the object's temperature (**Figure 2.2**). The hotter the object is, the more energetic the emitted photons and the shorter the wavelength. A hot surface such as that of the Sun (~5800°C) gives off primarily shortwave (solar) radiation. In contrast, cooler objects such as Earth's surface (average temperature of 15°C) emit radiation of longer wavelengths, or longwave (terrestrial) radiation.

Some of the shortwave radiation that reaches the surface of our planet is reflected back into space. The quantity of shortwave radiation reflected by a surface is a function of its reflectivity, referred to as its *albedo*. Albedo is expressed as a proportion (0–1.0) of the shortwave radiation striking a surface that is reflected and differs for different surfaces. For example, surfaces covered by ice and snow have a high albedo (0.8–0.9), reflecting anywhere from 80 to 90 percent of incoming solar

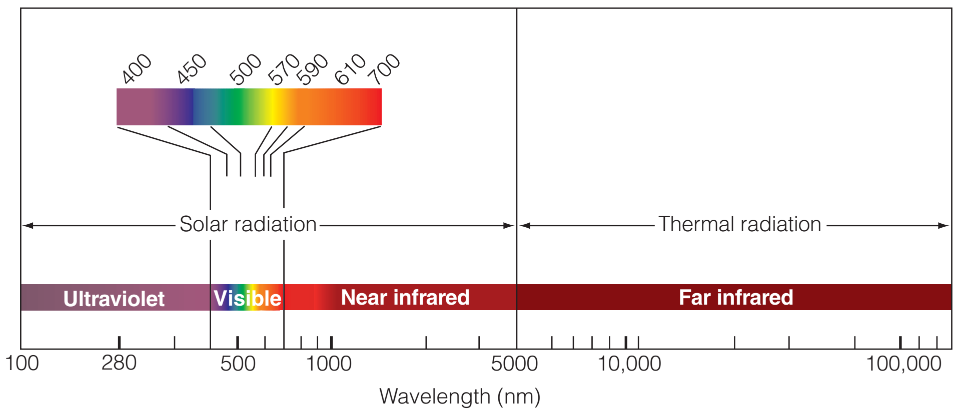
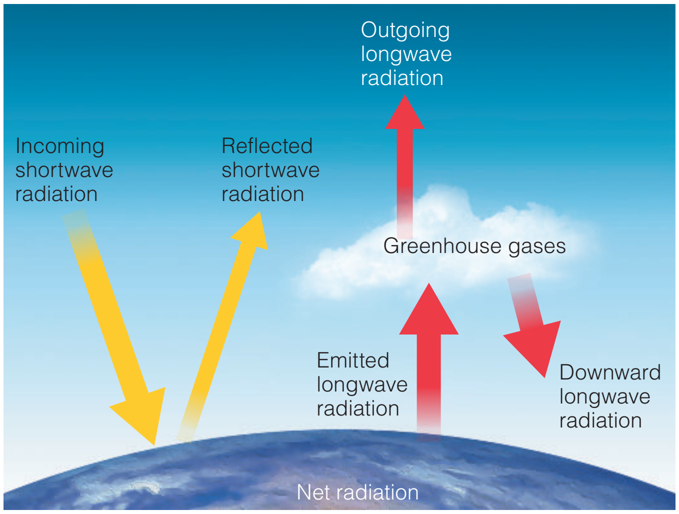


Figure 2.1 A portion of the electromagnetic spectrum, separated into solar (shortwave) and thermal (longwave) radiation. Ultraviolet, visible, and infrared light waves represent only a small part of the spectrum. To the left of ultraviolet radiation are X-rays and gamma rays (not shown).



Net radiation = (Incoming SW – Reflected SW)
– (Emitted LW – Downward LW)

Figure 2.3 Net radiation is the difference between the amount of shortwave (solar) radiation absorbed by a surface and the amount of longwave radiation emitted back into space by that surface. LW, longwave; SW, shortwave.

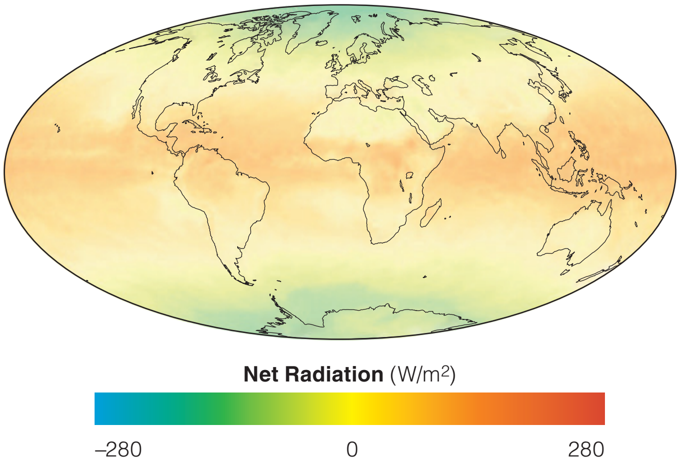


Figure 2.4 Global map of annual net radiation.

radiation, whereas a forest has a relatively low albedo (0.05), reflecting only 5 percent of sunlight. The global annual averaged albedo is approximately 0.30 (30 percent reflectance).

The difference between the incoming shortwave radiation and the reflected shortwave radiation is the net shortwave radiation absorbed by the surface. In turn, some of the energy absorbed by Earth's surface (both land and water) is emitted back out into space as terrestrial longwave radiation. The amount of energy emitted is dependent on the temperature of the surface. The hotter the surface, the more radiant energy it will emit. Most of the longwave radiation emitted by Earth's surface, however, is absorbed by water vapor and carbon dioxide in the atmosphere. This absorbed radiation is emitted downward toward the surface as longwave atmospheric radiation, which keeps near surface temperatures warmer than they would be without this blanket of gases. This is known as the "**greenhouse effect**," and gases such as water vapor and carbon dioxide that are good absorbers of longwave radiation are known as "**greenhouse gases**."

It is the difference between the incoming shortwave (solar) radiation and outgoing longwave (terrestrial) radiation that defines the **net radiation** (**Figure 2.3**) and determines surface temperatures. If the amount of incoming shortwave radiation exceeds the amount of outgoing longwave radiation, surface temperature increases. Conversely, surface temperature declines if the quantity of outgoing longwave radiation exceeds the incoming shortwave radiation (as is the case during the night). On average, the amount of incoming shortwave radiation intercepted by Earth and the quantity of longwave radiation emitted by the planet back into space balance, and the average surface temperature of our planet remains approximately 15ºC. Note, however, from the global map of average annual surface net radiation presented in **Figure 2.4** that there is a distinct latitudinal gradient of decreasing net surface radiation from the equator toward the poles. This decline is a direct function of the variation with latitude in the amount of shortwave radiation reaching the surface. Two factors influence this variation (**Figure 2.5**). First, at higher latitudes, solar radiation hits the surface at a steeper angle, spreading sunlight over a larger area. Second, solar radiation that penetrates the atmosphere at a steep angle must travel through a deeper layer of air. In the process, it encounters more particles in the atmosphere, which reflect more of the shortwave radiation back into space. The result of the decline in net radiation with latitude is a distinct gradient of decreasing mean annual temperature from the equator toward the poles (**Figure 2.6**).

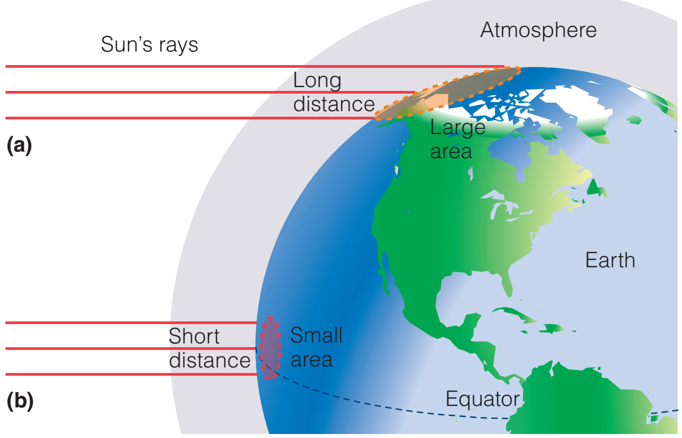


Figure 2.5 As one moves from the equator to the poles, there is a decrease in the average amount of solar (shortwave) radiation reaching Earth's surface. Two factors influence this variation. First, at higher latitudes (a), solar radiation hits the surface at a steeper angle, spreading sunlight over a larger area than at the equator (b). Second, solar radiation that penetrates the atmosphere at a steep angle must travel through a deeper layer of air.

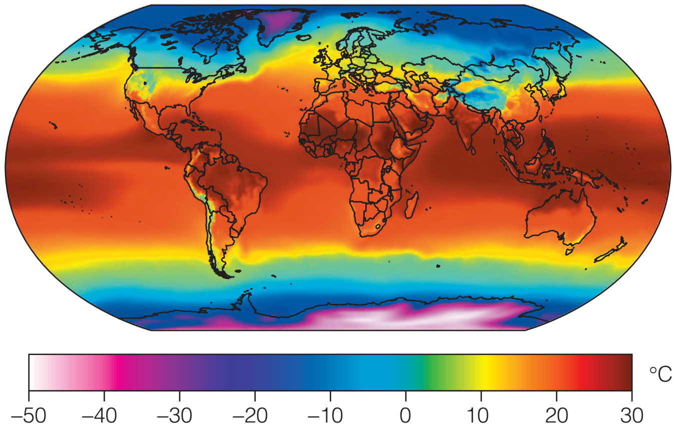


Figure 2.6 Global map of mean annual temperature (°C). Map based on annually averaged near-surface air temperature from 1961 to 1990.

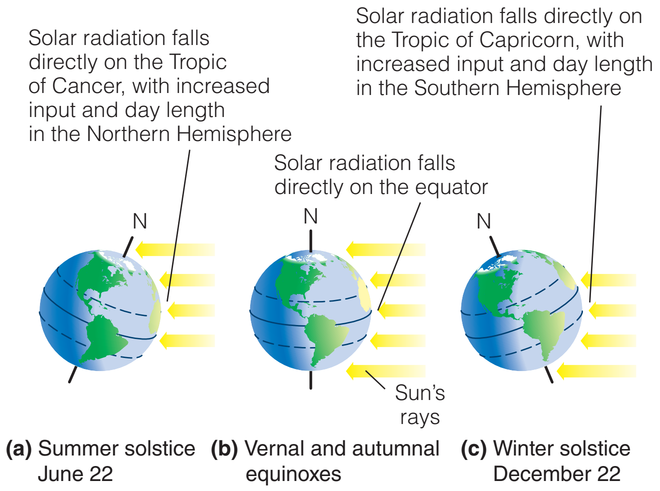


Figure 2.7 Changes in the angle of the Sun and circle of illumination during Earth's yearly orbit (equinoxes and the winter and summer solstices are illustrated). Note that as a result of the 23.5° tilt of Earth on its north–south axis, the point of Earth's surface where the Sun is directly overhead migrates from the tropic of Cancer (23.5° N) to the tropic of Capricorn (23.5° S) over the course of the year.

2.2 Intercepted Solar Radiation and Surface Temperatures Vary Seasonally

Although the variation in shortwave (solar) radiation reaching Earth's surface with latitude can explain the gradient of decreasing mean annual temperature from the equator to the poles, it does not explain the systematic variation occurring over the course of a year. What gives rise to the seasons on Earth? Why do the hot days of summer give way to the changing colors of fall, or the freezing temperatures and snow-covered landscape of winter to the blanket of green signaling the onset of spring? The explanation is quite simple: it is because Earth does not stand up straight but rather tilts to its side.

Earth, like all planets, is subject to two distinct motions. While it orbits the Sun, Earth rotates about an axis that passes through the North and South Poles, giving rise to the brightness of day followed by the darkness of night (the diurnal cycle). Earth travels about the Sun in an ecliptic plane. By chance, Earth's axis of spin is not perpendicular to the ecliptic plane but tilted at an angle of 23.5°. As a result, as Earth follows its elliptical orbit about the Sun, the location on the surface where the Sun is directly overhead at midday migrates between 23.5° N and 23.5° S latitude over the course of the year (**Figure 2.7**).

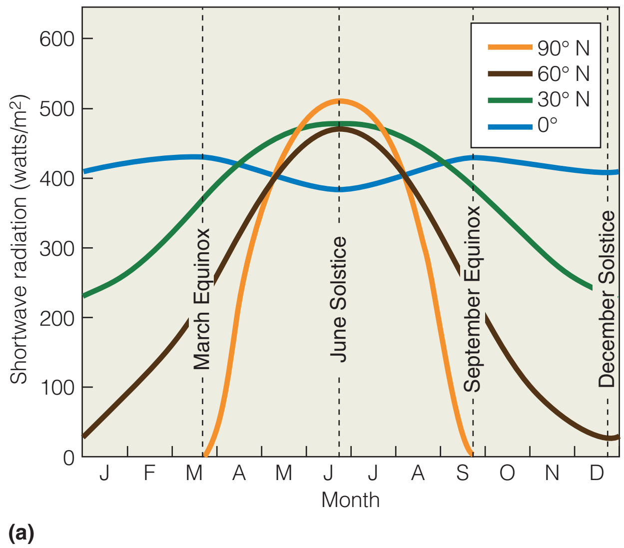
At the vernal equinox (approximately March 21) and autumnal equinox (approximately September 22), the Sun is directly overhead at the equator (see Figure 2.7). At this time, the equatorial region receives the greatest input of shortwave (solar) radiation, and every place on Earth receives the same 12 hours each of daylight and night.

At the summer solstice (approximately June 22) in the Northern Hemisphere, solar rays fall directly on the Tropic of Cancer (23.5° N; see Figure 2.7). This is when days are longest in the Northern Hemisphere, and the input of solar radiation to the surface is the greatest. In contrast, the Southern Hemisphere experiences winter at this time. At winter solstice (about December 22) in the Northern Hemisphere, solar rays fall directly on the Tropic of Capricorn (23.5° S; see Figure 2.7). This period is summer in the Southern Hemisphere, whereas the Northern Hemisphere is enduring shorter days and colder temperatures. Thus, the summer solstice in the Northern Hemisphere is the winter solstice in the Southern Hemisphere.

In the equatorial region there is little seasonality (variation over the year) in net radiation, temperature, or day length. Seasonality systematically increases from the equator to the poles (**Figure 2.8**). At the Arctic and Antarctic circles (66.5° N and S, respectively), day length varies from 0 to 24 hours over the course of the year. The days shorten until the winter solstice, a day of continuous darkness. The days lengthen with spring, and on the day of the summer solstice, the Sun never sets.

2.3 Geographic Difference in Surface Net Radiation Result in Global Patterns of Atmospheric Circulation

As we discussed in the previous section, the average net radiation of the planet is zero; that is to say that the amount of incoming shortwave radiation absorbed by the surface is offset by the quantity of outgoing longwave radiation back into space. Otherwise, the average temperature of the planet would either increase or decrease. Geographically, however, this is not the case. Note from the global map of mean annual net radiation presented in Figure 2.4 that there are regions of positive (surplus) and negative (deficit) net radiation. In fact, there is a distinct latitudinal pattern of surface radiation illustrated in



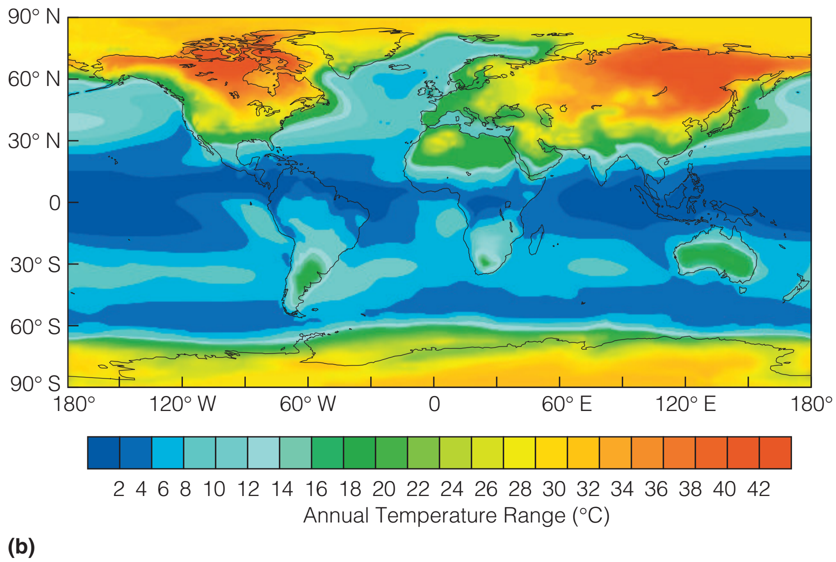


Figure 2.8 Two examples of changes in seasonality with latitude. (a) Annual variations in mean monthly solar (shortwave radiation) for different latitudes in the Northern Hemisphere. (b) Global map of annual temperature range, defined as the difference in temperature (°C) between the coldest and warmest month of the year (based on mean monthly temperatures for the period of 1979–2004).

Figure 2.9. Between 35.5° N and 35.5° S (from the equator to the midlatitudes), the amount of incoming shortwave radiation received over the year exceeds the amount of outgoing longwave radiation and there is a surplus. In contrast, from 35.5° N and S latitude to the poles (90° N and S), the amount of outgoing longwave radiation over the year exceeds the incoming shortwave radiation and there is a deficit. This imbalance in net radiation sets into motion a global scale pattern of the redistribution of thermal energy (heat) from the equator to the poles. Recall from basic physical sciences that energy flows from regions of higher concentration to regions of lower concentration, that is, from warmer regions to cooler regions. The primary mechanism of this planetary transfer of heat from the tropics (region of net radiation surplus) to the poles (region of net radiation deficit) is the process of convection, that is, the transfer of heat through the circulation of fluids (air and water).

As previously discussed, the equatorial region receives the largest annual input of solar radiation and greatest net radiation surplus. Air warmed at the surface rises because it is less dense than the cooler air above it. Air heated at the equatorial region rises to the top of the troposphere, establishing a zone of low pressure at the surface (**Figure 2.10**). This low atmospheric pressure at the surface causes air from the north and south to flow toward the equator (air moves from areas of higher pressure to areas of lower pressure). The resulting convergence of winds from the north and south in the region of the equator is called the *Intertropical Convergence Zone*, or *ITCZ*, for short.

The continuous column of rising air at the equator forces the air mass above to spread north and south toward the poles. As air masses move poleward, they cool, become heavier (more dense), and sink. The sinking air at the poles raises

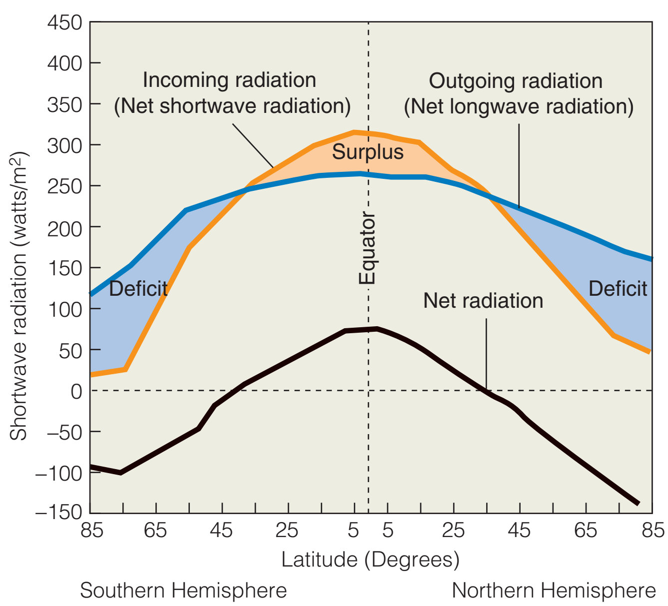


Figure 2.9 Variation in mean annual incoming shortwave radiation, outgoing longwave radiation, and net radiation as a function of latitude. Note that from the equator to approximately 35° N and S latitude, the amount of incoming shortwave radiation exceeds the amount of outgoing longwave radiation, and there is a net surplus of surface radiation (mean annual net radiation > 0). Conversely, there is a deficit (mean net radiation < 0) from 35° N and S to the poles (90° N and S). This gradient of net radiation drives the transport of heat from the tropics to the poles through the circulation of the atmosphere and oceans.

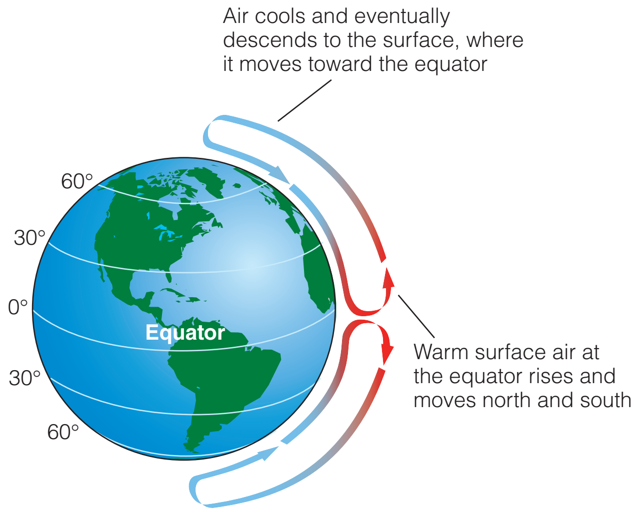


Figure 2.10 Circulation of air cells and prevailing winds on an imaginary, nonrotating Earth. Air heated at the equator rises and moves north and south creating a zone of low pressure at the surface. After cooling at the poles, it descends, creating a high pressure zone at the poles causing air to flow back toward the equator.

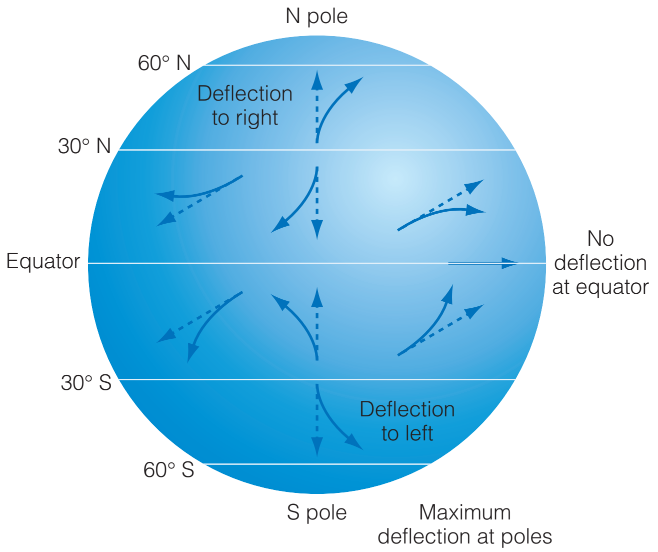


Figure 2.11 Effect of the Coriolis force on wind direction. The effect is absent at the equator, where the linear velocity is the greatest, 465 meters per second (m/s; 1040 mph). Any object on the equator is moving at the same rate. The Coriolis effect increases regularly toward the poles. If an object, including an air mass, moves northward from the equator at a constant speed, it speeds up because Earth moves more slowly (403 m/s at 30° latitude, 233 m/s at 60° latitude, and 0 m/s at the poles) than the object does. As a result, the object's path appears to deflect to the right or east in the Northern Hemisphere and to the left or west in the Southern Hemisphere.

surface air pressure, forming a high-pressure zone and creating a pressure gradient from the poles to the equator. The cooled, heavier air then flows toward the low-pressure zone at the equator, replacing the warm air rising over the tropics and closing the pattern of air circulation. If Earth were stationary and without irregular landmasses, the atmosphere would circulate as shown in Figure 2.10. Earth, however, spins on its axis from west to east. Although each point on Earth's surface makes a complete rotation every 24 hours, the speed of rotation varies with latitude (and circumference). At a point on the equator (its widest circumference at 40,176 km), the speed of rotation is 1674 km per hour. In contrast, at 60° N or S, Earth's circumference is approximately half that at the equator (20,130 km), and the speed of rotation is 839 km per hour. According to the law of angular motion, the momentum of an object moving from a greater circumference to a lesser circumference will deflect in the direction of the spin, and an object moving from a lesser circumference to a greater circumference will deflect in the direction opposite that of the spin. As a result, air masses and all moving objects in the Northern Hemisphere are deflected to the right (clockwise motion), and in the Southern Hemisphere to the left (counterclockwise motion). This deflection in the pattern of air flow is the **Coriolis effect**, named after the 19th-century French mathematician G. C. Coriolis, who first analyzed the phenomenon (**Figure 2.11**).

In addition to the deflection resulting from the Coriolis effect, air that moves poleward is subject to longitudinal compression, that is, poleward-moving air is forced into a smaller space, and the density of the air increases. These factors prevent a direct, simple flow of air from the equator to the poles. Instead, they create a series of belts of prevailing winds, named for the direction they come from. These belts break the simple flow of surface air toward the equator and they flow aloft to the poles into a series of six cells, three in each hemisphere. They produce areas of low and high pressure as air masses ascend from and descend toward the surface, respectively (**Figure 2.12**). To trace the flow of air as it circulates between the equator and poles, we begin at Earth's equatorial region, which receives the largest annual input of solar radiation.

Air heated in the equatorial zone rises upward, creating a low-pressure zone near the surface—the **equatorial low**. This upward flow of air is balanced by a flow of air from the

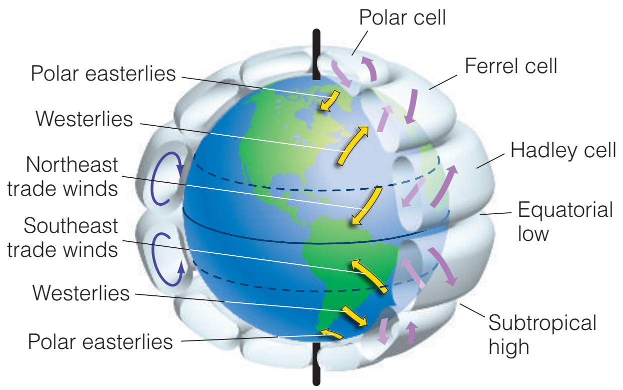


Figure 2.12 Belts and cells of air circulation about a rotating Earth. This circulation gives rise to the trade, westerly, and easterly winds.

north and south toward the equator (ITCZ). As the warm air mass rises, it begins to spread, diverging northward and southward toward the North and South Poles, cooling as it goes. In the Northern Hemisphere, the Coriolis effect forces air in an easterly direction, slowing its progress north. At about 30° N, the now-cool air sinks, closing the first of the three cells—the Hadley cells, named for the Englishman George Hadley, who first described this pattern of circulation in 1735. The descending air forms a semipermanent high-pressure belt at the surface that encircles Earth—the **subtropical high**. Having descended, the cool air warms and splits into two currents flowing over the surface. One moves northward toward the pole, diverted to the right by the Coriolis effect to become the prevailing **westerlies**. Meanwhile, the other current moves southward toward the equator. Also deflected to the right, this southward-flowing stream becomes the strong, reliable winds that were called **trade winds** by the 17th-century merchant sailors who used them to reach the Americas from Europe. In the Northern Hemisphere, these winds are known as the *northeast trades*. In the Southern Hemisphere, where similar flows take place, these winds are known as the *southeast trades*.

As the mild air of the westerlies moves poleward, it encounters cold air moving down from the pole (approximately 60° N). These two air masses of contrasting temperature do not readily mix. They are separated by a boundary called the *polar front*—a zone of low pressure (the **subpolar low**) where surface air converges and rises. Some of the rising air moves southward until it reaches approximately 30° latitude (the region of the subtropical high), where it sinks back to the surface and closes the second of the three cells—the Ferrel cell, named after U.S. meteorologist William Ferrel.

As the northward-moving air reaches the pole, it slowly sinks to the surface and flows back (southward) toward the polar front, completing the last of the three cells—the polar cell. This southward-moving air is deflected to the right by the Coriolis effect, giving rise to the **polar easterlies**. Similar flows occur in the Southern Hemisphere (see Figure 2.12).

This pattern of global atmospheric circulation functions to transport heat (thermal energy) from the tropics (the region of net radiation surplus) toward the poles (the regions of net radiation deficit), moderating temperatures at the higher latitudes.

2.4 Surface Winds and Earth's Rotation Create Ocean Currents

The global pattern of prevailing winds plays a crucial role in determining major patterns of surface water flow in Earth's oceans. These systematic patterns of water movement are called *currents*. In fact, until they encounter one of the continents, the major ocean currents generally mimic the movement of the surface winds presented in the previous section.

Each ocean is dominated by two great circular water motions, or **gyres**. Within each gyre, the ocean current moves clockwise in the Northern Hemisphere and counterclockwise in the Southern Hemisphere (**Figure 2.13**). Along the equator, trade winds push warm surface waters westward. When these waters encounter the eastern margins of continents, they split into north- and south-flowing currents along the coasts, forming north and south gyres. As the currents move farther from the equator, the water cools. Eventually, they encounter the westerly winds at higher latitudes (30–60° N

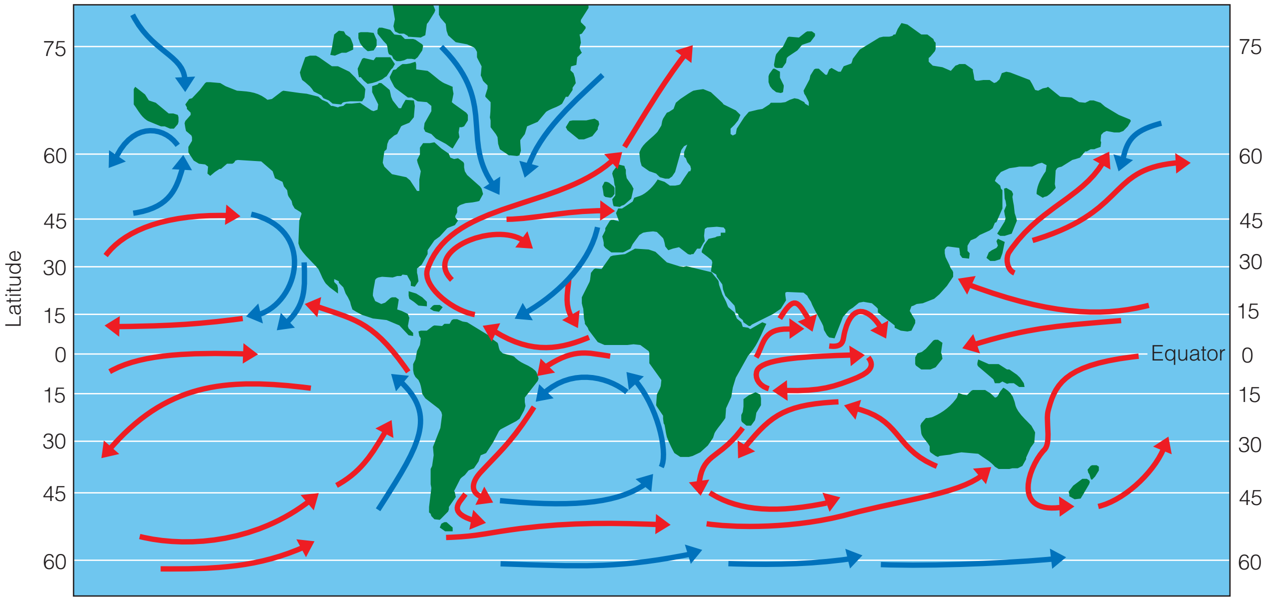


Figure 2.13 Ocean currents of the world. Notice how the circulation is influenced by the Coriolis force (clockwise movement in the Northern Hemisphere and counterclockwise movement in the Southern Hemisphere) and continental landmasses, and how oceans are connected by currents. Blue arrows represent cool water, and red arrows represent warm water.

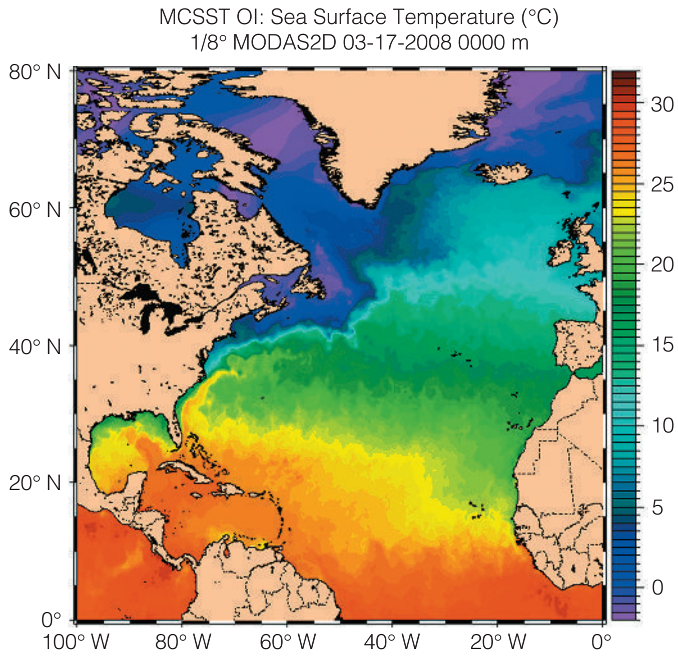


Figure 2.14 Color enhanced satellite image of the Gulf Steam current in the North Atlantic Ocean. Surface water temperatures increase from blue-green-yellow to red. The Gulf Stream carries warm tropical waters northward along the east coast of North America and into the cold waters of the North Atlantic moderating temperatures in Western Europe.

and 30–60° S), which produce eastward-moving currents. When these eastward-moving currents encounter the western margins of the continents, they form cool currents that flow along the coastline toward the equator. Just north of the Antarctic continent, ocean waters circulate unimpeded around the globe.

As with the patterns of global atmospheric circulation and winds, the gyres function to redistribute heat from the tropics northward and southward toward the poles (**Figure 2.14**).

2.5 Temperature Influences the Moisture Content of Air

Air temperature plays a crucial role in the exchange of water between the atmosphere and Earth's surface. Whenever matter, including water, changes from one state to another, energy is either absorbed or released. The amount of energy released or absorbed (per gram) during a change of state is known as *latent heat* (from the Latin *latens*, "hidden"). In going from a more ordered state (liquid) to a less ordered state (gas), energy is absorbed (the energy required to break bonds between molecules). While going from a less ordered to a more ordered state, energy is released. Evaporation, the transformation of water from a liquid to a gaseous state, requires 2260 joules (J) of energy per gram of liquid water to be converted to water vapor (1 joule is the equivalent of 1 watt of power radiated or dissipated for 1 second). Condensation, the transformation of water vapor to a liquid state, releases an equivalent amount of energy. When air comes into contact with liquid water, water molecules are freely exchanged between the air and the water's surface. When the evaporation rate equals the condensation rate, the air is said to be saturated. In the air, water vapor acts as an independent gas that has weight and exerts pressure. The amount of pressure that water vapor exerts independent of the pressure of dry air is called vapor pressure. Vapor pressure is typically defined in units of pascals (Pa). The water vapor content of air at saturation is called the *saturation vapor pressure*. The saturation vapor pressure, also known as the *water vapor capacity of air*, cannot be exceeded. If the vapor pressure exceeds the capacity, condensation occurs and reduces the vapor pressure. Saturation vapor pressure varies with temperature, increasing as air temperature increases (**Figure 2.15**). Having a greater quantity of thermal energy to support evaporation, warm air has a greater capacity for water vapor than does cold air.

The amount of water in a given volume of air is its absolute humidity. A more familiar measure of the water content of the air is **relative humidity**, or the amount of water vapor in the air expressed as a percentage of the saturation vapor pressure. At saturation vapor pressure, the relative humidity is 100 percent. If air cools while the actual moisture content (water vapor pressure) remains constant, then relative humidity increases as the value of saturation vapor pressure

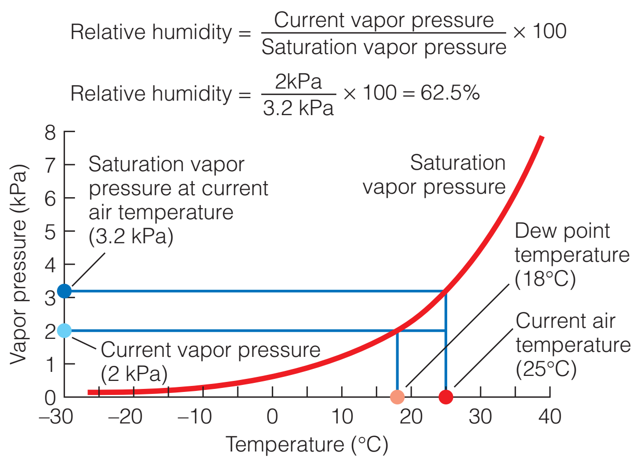


Figure 2.15 Saturation vapor pressure (VP) as a function of air temperature (saturation VP increases with air temperature). For a given air temperature, the relative humidity is the ratio of current VP to saturation VP (current VP/saturation VP) × 100. For a given VP, the temperature at which saturation VP occurs is called the dew point.

Interpreting Ecological Data

Q1. *Assume that the actual (current) water vapor pressure remains the same over the course of the day and that the current air temperature of 25°C in the above graph represents the air temperature at noon (12:00 p.m.). How would you expect the relative humidity to change from noon to 5:00 p.m.? Why?*

Q2. *What is the approximate relative humidity at 35°C? (Assume that actual water vapor pressure remains the same as in the above figure, 2 kilopascals [kPa].)*

declines. If the air cools to a point where the actual vapor pressure is equal to the saturation vapor pressure, moisture in the air will condense. This is what occurs when a warm parcel of air at the surface becomes buoyant and rises. As it rises, it cools, and as it cools, the relative humidity increases. When the relative humidity reaches 100 percent, water vapor condenses and forms clouds. As soon as particles of water or ice in the air become too heavy to remain suspended, precipitation falls. For a given water content of a parcel of air (vapor pressure), the temperature at which saturation vapor pressure is achieved (relative humidity is 100 percent) is called the **dew point temperature**. Think about finding dew or frost on a cool fall morning. As nightfall approaches, temperatures drop and relative humidity rises. If cool night air temperatures reach the dew point, water condenses and dew forms, lowering the amount of water in the air. As the sun rises, air temperature warms and the water vapor capacity (saturation vapor pressure) increases. As a result, the dew evaporates, increasing vapor pressure in the air.

2.6 Precipitation Has a Distinctive Global Pattern

By bringing together patterns of temperature, winds, and ocean currents, we are ready to understand the global pattern of precipitation. Precipitation is not evenly distributed across Earth (**Figure 2.16**). At first the global map of annual precipitation in Figure 2.16 may seem to have no discernible pattern or regularity. But if we examine the simpler pattern of variation in average rainfall with latitude (**Figure 2.17**), a general pattern emerges. Precipitation is highest in the region of the equator, declining as one moves north and south. The decline, however, is not continuous. Two troughs occur in the midlatitudes interrupting the general patterns of decline in precipitation from the equator toward the poles. The sequence of peaks and troughs seen in Figure 2.17 corresponds to the pattern of rising and falling air masses associated with the belts of prevailing winds presented in Figure 2.12.

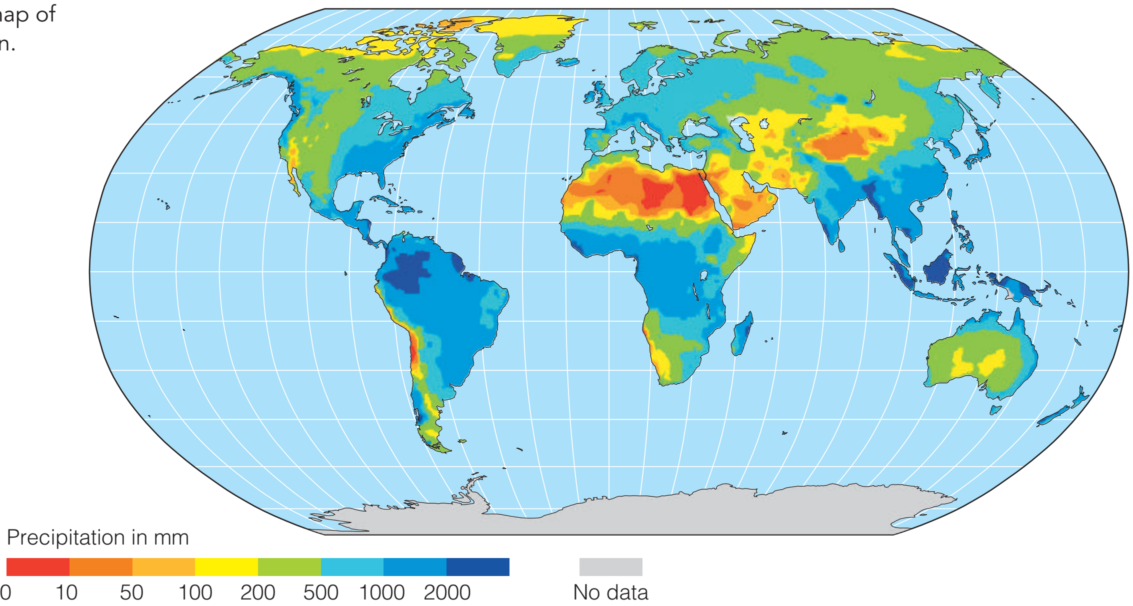
As the warm trade winds move across the tropical oceans, they gather moisture. Near the equator, the northeasterly trade winds meet the southeasterly trade winds. This narrow region where the trade winds meet is the ITCZ, characterized by high amounts of precipitation. Where the two air masses meet, air piles up, and the warm humid air rises and cools. When the dew point is reached, clouds form, and precipitation falls as rain. This pattern accounts for high precipitation in the tropical regions of eastern Asia, Africa, and South and Central America (see Figure 2.16).

Having lost much of its moisture, the ascending air mass continues to cool as it splits and moves northward and southward. In the region of the subtropical high (approximately 30° N and S), where the cool air descends, two belts of dry climate encircle the globe (the two troughs at the midlatitudes seen in Figure 2.17). The descending air warms. Because the saturation vapor pressure rises, it draws water from the surface through evaporation, causing arid conditions. In these belts, the world's major deserts have formed (see Chapter 23).

As the air masses continue to move north and south, they once again draw moisture from the surface, but to a lesser degree because of the cooler surface conditions. Moving poleward, they encounter cold air masses originating at the poles (approximately 60° N and S). Where the surface air masses converge and rise, the ascending air mass cools and precipitation occurs (seen as the two smaller peaks in precipitation between 50° and 60° N and S in Figure 2.17). From this point on to the poles, the cold temperature and associated low-saturation vapor pressure function to restrict precipitation.

One other pattern is worth noting in Figure 2.17. In general, rainfall is greater in the Southern Hemisphere than in the

Figure 2.16 Global map of mean annual precipitation. (Goddard Institute for Space Studies (GISS) - NASA Lab.)



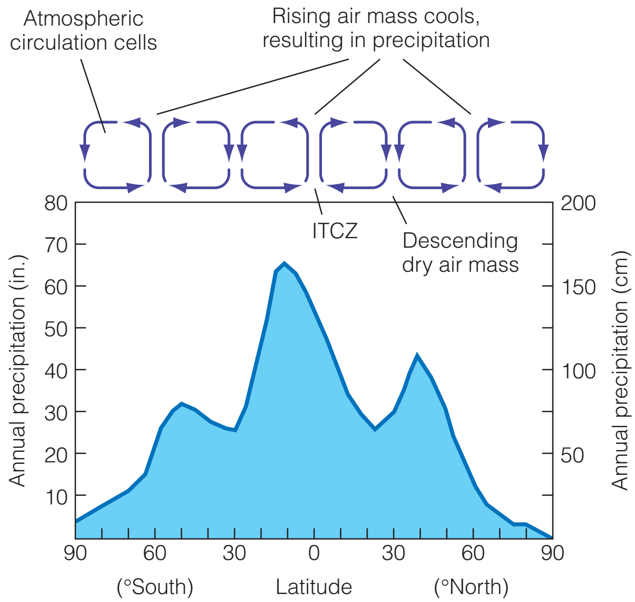


Figure 2.17 Variation in mean annual precipitation with latitude. The peaks in rainfall correspond to rising air masses, whereas the troughs are associated with descending dry air masses.

Northern Hemisphere (note the southern shift in the rainfall peak associated with the ITCZ). This is because the oceans cover a greater proportion of the Southern Hemisphere, and water evaporates more readily from the water's surface than from the soil and vegetation.

Missing from our discussion thus far is the temporal variation of precipitation over Earth. The temporal variation is directly linked to the seasonal changes in the surface radiation balance of Earth and its effect on the movement of global pressure systems and air masses. This is illustrated in seasonal movement north and south of the ITCZ, which follows the apparent migration of the direct rays of the Sun (**Figure 2.18**).

The ITCZ is not stationary but tends to migrate toward regions of the globe with the warmest surface temperature. Although tropical regions around the equator are always exposed to warm temperatures, the Sun is directly over the geographical equator only twice a year, at the spring and fall equinoxes. At the northern summer solstice, the Sun is directly over the Tropic of Cancer; at the winter solstice (which is summer in the Southern Hemisphere), the Sun is directly over the Tropic of Capricorn. As a result, the ITCZ moves poleward and invades the subtropical highs in northern summer; in the winter it moves southward, leaving clear, dry weather behind. As the ITCZ migrates southward, it brings rain to the southern summer. Thus, as the ITCZ shifts north and south, it brings on the wet and dry seasons in the tropics (**Figure 2.19**).

2.7 Proximity to the Coastline Influences Climate

At the continental scale, an important influence on climate is the relationship between land and water. Land surfaces heat and cool more rapidly than water as a result of differences in their specific heat. Specific heat is the amount of thermal energy necessary to raise the temperature of one gram of a substance by 1°C. The specific heat of water is much higher than that of land or air. It takes approximately four times the amount of thermal energy to raise the temperature of water by 1°C than land or air. As a result, land areas farther from the coast (or other large bodies of water) experience a greater seasonal variation in temperature than do coastal areas (**Figure 2.20**). This pattern is referred to as **continentality**. Annual differences of as much as 100°C (from 50°C to –50°C) have been recorded in some locations.

The converse effect occurs in coastal regions. These locations have smaller temperature ranges as a result of what is called a *maritime influence*. Summer and winter extremes are moderated by the movement onshore of prevailing westerly wind systems from the ocean. Ocean currents minimize seasonal variations in the surface temperature of the water. The moderated water temperature serves to moderate temperature changes in the air mass above the surface.

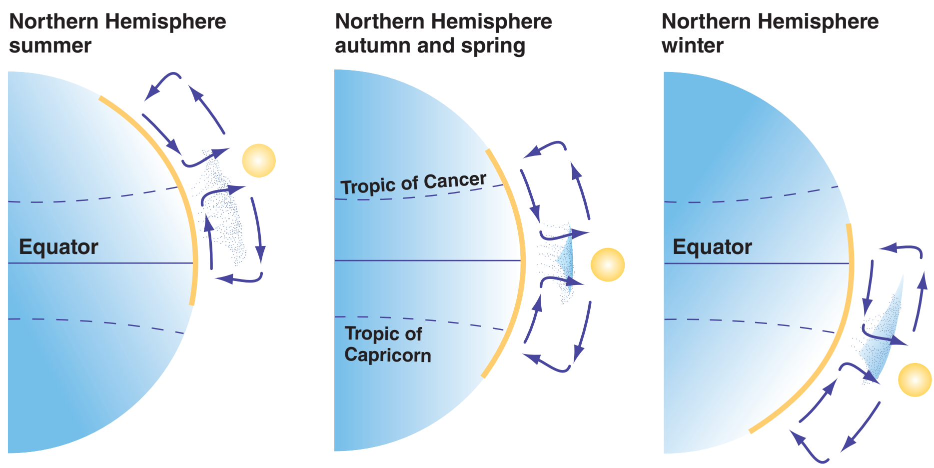


Figure 2.18 Shifts of the Intertropical Convergence Zone (ITCZ), producing seasonality in precipitation—rainy seasons and dry seasons. As the distance from the equator increases, the dry season is longer and the rainfall is less. These oscillations result from changes in the Sun's altitude between the equinoxes and the solstices, as diagrammed in Figure 2.7.

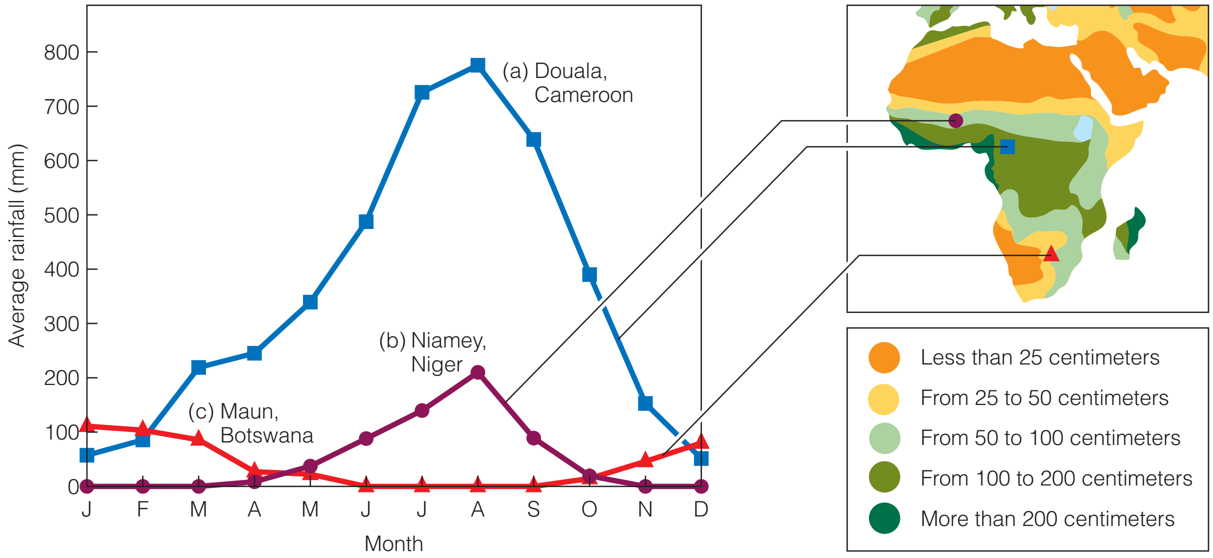


Figure 2.19 Seasonal variations in precipitation at three sites within the Intertropical Convergence Zone (ITCZ). Although site (a) shows a seasonal variation, precipitation exceeds 50 mm each month. Sites (b) and (c) are in the ITCZ regions that experience a distinct wet (summer) and dry (winter) season. The rainy season is six months out of phase for these two sites, reflecting the difference in the timing because the summer months occur at different times in the two hemispheres.

Proximity to large water bodies also tends to have a positive influence on precipitation levels. The interior of continents generally experience less precipitation than the coastal regions do. As air masses move inland from the coast, water vapor lost from the atmosphere through precipitation is not recharged (from surface evaporation) as readily as it is over the open waters of the ocean (note the gradients of precipitation from the coast to the interiors of North America and Europe/Asia in Figure 2.16). There are, however, notable exceptions to this rule, including the dry coast of southern California and the Arctic coastline of Alaska.

2.8 Topography Influences Regional and Local Patterns of Climate

Mountainous topography influences local and regional patterns of climate. Most obvious is the relationship between elevation and temperature. In the lower regions of the atmosphere (up to altitudes of approximately 12 km), temperature decreases with altitude at a fairly uniform rate because of declining air density and pressure. In addition, the atmosphere is warmed by conduction (transfer of heat through direct contact) from Earth's surface. So temperature declines with increasing distance from the conductive source (i.e., the surface). The rate of decline in temperature with altitude is called the **lapse rate**. So for the same latitude or proximity to the coast, locales at higher elevation will have consistently lower temperatures than those of lower elevation.

Mountains also influence patterns of precipitation. As an air mass reaches a mountain, it ascends, cools, relative

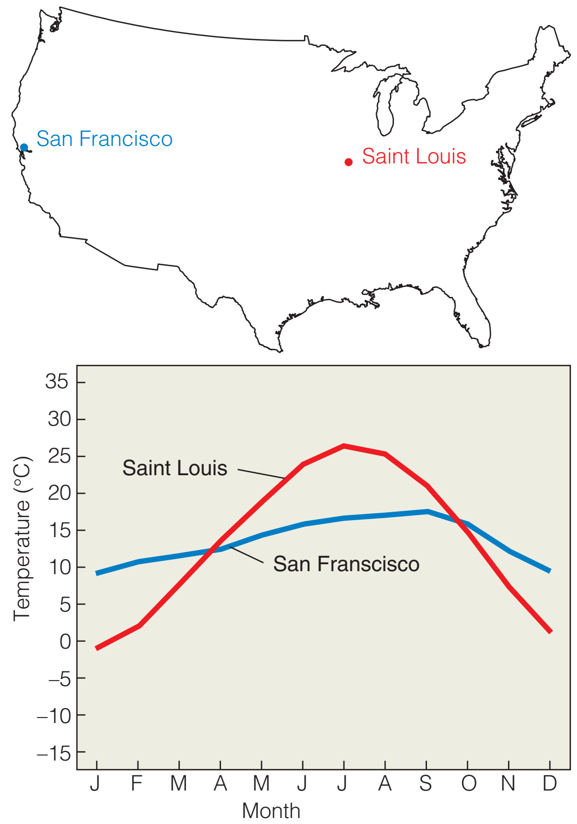


Figure 2.20 Pattern of mean monthly temperature (°C) for two locations in North America: San Francisco is located on the Pacific coast, whereas Saint Louis is in the middle of the continent.

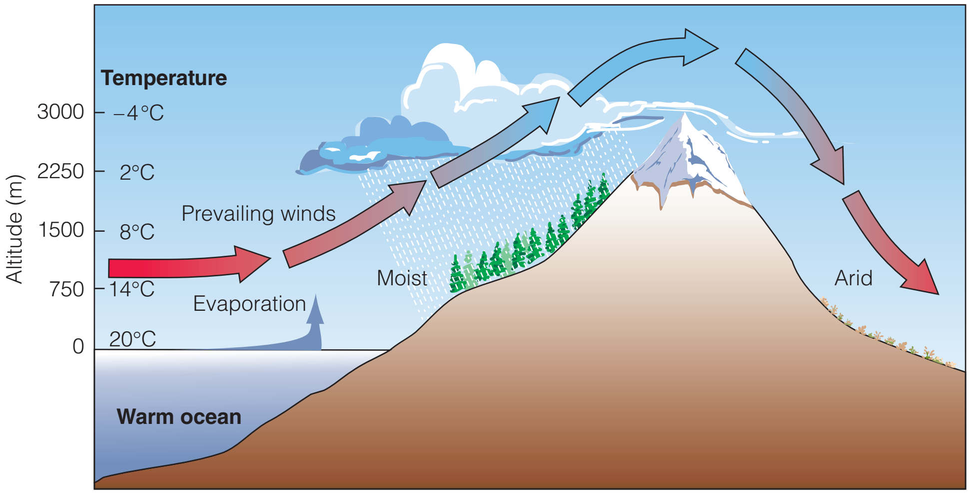


Figure 2.21 Formation of a rain shadow. Air is forced to go over a mountain. As it rises, the air mass cools and loses its moisture as precipitation on the windward side. The descending air, already dry, picks up moisture from the leeward side.

humidity rises (because of lower saturation vapor pressure). When the temperature cools to the dew point temperature, precipitation occurs at the upper altitudes of the windward side. As the now cool, dry air descends the leeward side, it warms again and relative humidity declines. As a result, the windward side of a mountain supports denser, more vigorous vegetation and different species of plants and associated animals than does the leeward side, where in some areas dry, desert-like conditions exist. This phenomenon is called a **rain shadow** (**Figure 2.21**). Thus, in North America, the westerly winds that blow over the Sierra Nevada and the Rocky Mountains, dropping their moisture on west-facing slopes, support vigorous forest growth. By contrast, the eastern slopes exhibit semidesert or desert conditions.

Some of the most pronounced effects of this same phenomenon occur in the Hawaiian Islands. There, plant cover ranges from scrubby vegetation on the leeward side of an island to moist, forested slopes on the windward side (**Figure 2.22**).

2.9 Irregular Variations in Climate Occur at the Regional Scale

The patterns of temporal variation in climate that we have discussed thus far occur at regular and predictable intervals: seasonal changes in temperature with the rotation of Earth around the Sun, and migration of the ITCZ with the resultant seasonality of rainfall in the tropics and monsoons in Southeast Asia. Not all features of the climate system, however, occur so regularly. Earth's climate system is characterized by variability at both the regional and global scales. The Little Ice Age, a period of cooling that lasted from approximately the mid-14th to the mid-19th century, brought bitterly cold winters to many parts of the Northern Hemisphere, affecting agriculture, health, politics, economics, emigration, and even art and literature. In the mid-17th century, glaciers in the Swiss Alps advanced, gradually engulfing farms and crushing entire villages. In 1780, New York Harbor froze, allowing people to walk from Manhattan to Staten Island. In fact, the image of a white Christmas evoked by Charles Dickens and the New England poets of the 18th and 19th centuries is largely a product of the cold and snowy winters of the Little Ice Age. But the climate has since warmed to the point that a white Christmas in these regions is becoming an anomaly.

The Great Plains region of central North America has undergone periods of drought dating back to the mid-Holocene period some 5000 to 8000 years ago, but the homesteaders of the early 20th century settled the Great Plains at a time of relatively wet summers. They assumed these moisture conditions were the norm, and they employed the agricultural methods they had used in the East. So they broke the prairie sod for crops, but the cycle of drought returned, and the prairie grasslands became a dust bowl (see Chapter 4, *Ecological Issues & Applications*).

These examples reflect the variability in Earth's climate systems, which operate on timescales ranging from decades

Figure 2.22 Rain shadow on the mountains of Maui, Hawaiian Islands. The windward, east-facing slopes intercept the trade winds and are cloaked with wet forest (left). Low-growing, shrubby vegetation is found on the dry side (right).

to tens of thousands of years, driven by changes in the input of energy to Earth's surface (see Section 2.1). Earth's orbit is not permanent. Changes occur in the tilt of the axis and the shape of the yearly path about the Sun. These variations affect climate by altering the seasonal inputs of solar radiation. Occurring on a timescale of tens of thousands of years, these variations are associated with the glacial advances and retreats throughout Earth's history (see Chapter 18).

Variations in the level of solar radiation to Earth's surface are also associated with sunspot activity—huge magnetic storms on the Sun. These storms are associated with strong solar emissions and occur in cycles, with the number and size reaching a maximum approximately every 11 years. Researchers have related sunspot activity, among other occurrences, to periods of drought and winter warming in the Northern Hemisphere.

Interaction between two components of the climate system, the ocean and the atmosphere, are connected to some major climatic variations that occur at a regional scale. As far back as 1525, historic documents reveal that fishermen off the coast of Peru recorded periods of unusually warm water. The Peruvians referred to these as El Niño because they commonly appear at Christmastime, the season of the Christ Child (Spanish: *El Niño*). Now referred to by scientists as the El Niño–Southern Oscillation (ENSO), this phenomenon is a global event arising from large-scale interaction between the ocean and the atmosphere. The Southern Oscillation, a more recent discovery, refers to an oscillation in the surface pressure (atmospheric mass) between the southeastern tropical Pacific and the Australian-Indonesian regions. When the waters of the eastern Pacific are abnormally warm (an El Niño event), sea level pressure drops in the eastern Pacific and rises in the west. The reduction in the pressure gradient is accompanied by a weakening of the low-latitude easterly trades.

Although scientists still do not completely understand the cause of the ENSO phenomenon, its mechanism has been well documented. Recall from Section 2.3 that the trade winds blow westward across the tropical Pacific (see Figure 2.12). As a consequence, the surface currents within the tropical oceans flow westward (see Figure 2.14), bringing cold, deeper waters to the surface off the coast of Peru in a process known as upwelling (see Section 3.8). This pattern of upwelling, together with the cold-water current flowing from south to north along the western coast of South America, results in this region of the ocean usually being colder than one would expect given its equatorial location (**Figure 2.23**).

As the surface currents move westward the water warms, giving the water's destination, the western Pacific, the warmest ocean surface on Earth. The warmer water of the western Pacific causes the moist maritime air to rise and cool, bringing abundant rainfall to the region (Figure 2.23; also see Figure 2.16). In contrast, the cooler waters of the eastern Pacific result in relatively dry conditions along the Peruvian coast.

During an El Niño event, the trade winds slacken, reducing the westward flow of the surface currents (see Figure 2.23). The result is a reduced upwelling and a warming of the surface waters in the eastern Pacific. Rainfall follows the warm water eastward, with associated flooding in Peru and drought in Indonesia and Australia.

This eastward displacement of the atmospheric heat source (latent heat associated with the evaporation of water; see Section 3.2) overlaying the warm surface waters results in large changes in global atmospheric circulation, in turn influencing weather in regions far removed from the tropical Pacific.

At other times, the injection of cold water becomes more intense than usual, causing the surface of the eastern Pacific to cool. This variation is referred to as La Niña (**Figure 2.24**). It results in droughts in South America and heavy rainfall, even floods, in eastern Australia.

2.10 Most Organisms Live in Microclimates

Most organisms live in local conditions that do not match the general climate profile of the larger region surrounding them. For example, today's weather report may state that the temperature is 28°C and the sky is clear. However, your weather forecaster is painting only a general picture. Actual conditions of specific environments will be quite different depending on whether they are underground versus on the surface, beneath vegetation or on exposed soil, or on mountain slopes or at the seashore. Light, heat, moisture, and air movement all vary greatly from one part of the landscape to another, influencing the transfer of heat energy and creating a wide range of localized climates. These microclimates define the conditions organisms live in.

On a sunny but chilly day in early spring, flies may be attracted to sap oozing from the stump of a maple tree. The flies are active on the stump despite the near-freezing air temperature because, during the day, the surface of the stump absorbs solar radiation, heating a thin layer of air above the surface. On a still day, the air heated by the tree stump remains close to the surface, and temperatures decrease sharply above and below this layer. A similar phenomenon occurs when the frozen surface of the ground absorbs solar radiation and thaws. On a sunny, late winter day, the ground is muddy even though the air is cold.

By altering soil temperatures, moisture, wind movement, and evaporation, vegetation moderates microclimates, especially areas near the ground. For example, areas shaded by plants have lower temperatures at ground level than do places exposed to the Sun. On fair summer days in locations 25 millimeters (mm; 1 inch) aboveground, dense forest cover can reduce the daily range of temperatures by 7°C to 12°C below the soil temperature in bare fields. Under the shelter of heavy grass and low plant cover, the air at ground level is completely calm. This calm is an outstanding feature of microclimates within dense vegetation at Earth's surface. It influences both temperature and humidity, creating a favorable environment for insects and other ground-dwelling animals.

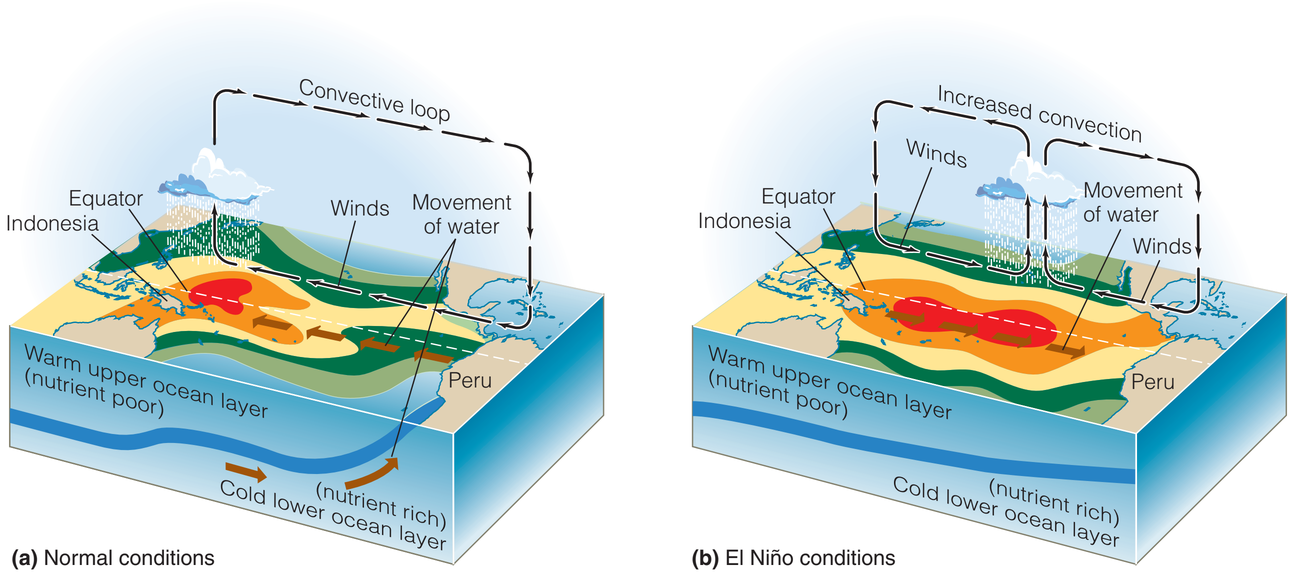


Figure 2.23 Schematic of the El Niño–Southern Oscillation (ENSO) that occurs off the western coast of South America. Under normal conditions, strong trade winds move surface waters westward (a). As the surface currents move westward, the water warms. The warmer water of the western Pacific causes the moist maritime air to rise and cool, bringing abundant rainfall to the region. Under ENSO conditions, the trade winds slacken, reducing the westward flow of the surface currents (b). Rainfall follows the warm water eastward, with associated flooding in Peru and drought in Indonesia and Australia.

Topography, particularly aspect (the direction that a slope faces), influences the local climatic conditions. In the Northern Hemisphere, south-facing slopes receive the most solar energy, whereas north-facing slopes receive the least (**Figure 2.25**). At other slope positions, energy received varies between these extremes, depending on their compass direction.

Different exposure to solar radiation at south- and north-facing sites has a marked effect on the amount of moisture and heat present. Microclimate conditions range from warm, dry, variable conditions on the south-facing slope to cool, moist, more uniform conditions on the north-facing slope. Because high temperatures and associated high rates of evaporation

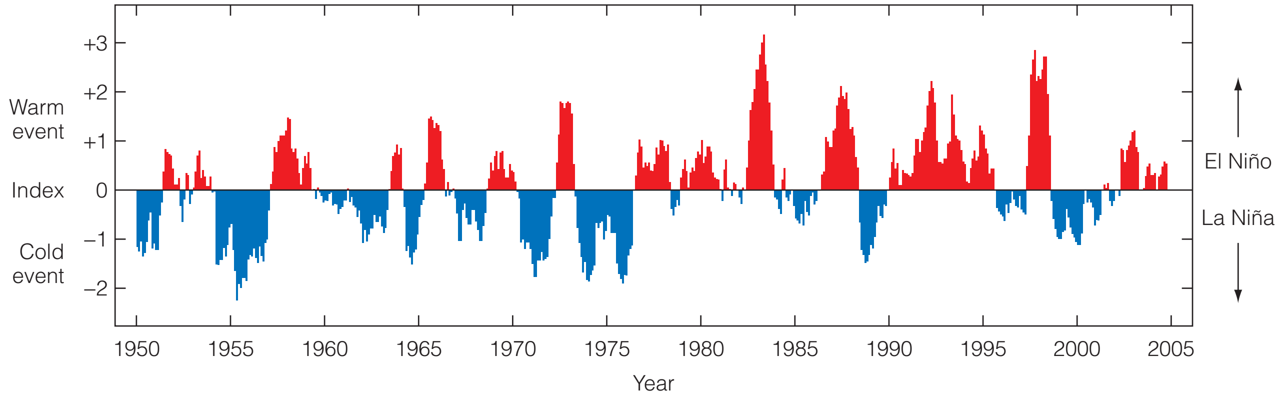


Figure 2.24 Record of El Niño–La Niña events during the second half of the 20th century. Numbers at the left of the diagram represent the ENSO index, which includes a combination of six factors related to environmental conditions over the tropical Pacific Ocean: air temperature, surface water temperature, sea-level pressure, cloudiness, and wind speed and direction. Warm episodes are in red; cold episodes are in blue. An index value greater than +1 represents an El Niño. A value less than −1 represents a La Niña.

draw moisture from soil and plants, the evaporation rate at south-facing slopes is often 50 percent higher, the average temperature is higher, and soil moisture is lower. Conditions are driest on the tops of south-facing slopes, where air movement is greatest, and dampest at the bottoms of north-facing slopes.

The same microclimatic conditions occur on a smaller scale on north- and south-facing slopes of large ant hills, mounds of soil, dunes, and small ground ridges in otherwise flat terrain, as well as on the north- and south-facing sides of buildings, trees, and logs. The south-facing sides of buildings are always warmer and drier than the north-facing sides—a consideration for landscape planners, horticulturists, and gardeners. North sides of tree trunks are cooler and moister than south sides, as reflected by more vigorous growth of moss on the north sides. In winter, the temperature of the north-facing side of a tree may be below freezing while the south side, heated by the Sun, is warm. This temperature difference may cause frost cracks in the bark as sap, thawed by day, freezes at night. Bark beetles and other wood-dwelling insects that seek cool, moist areas for laying their eggs prefer north-facing locations. Flowers on the south side of tree crowns often bloom sooner than those on the north side.

Microclimatic extremes also occur in depressions in the ground and on the concave surfaces of valleys, where the air is protected from the wind. Heated by sunlight during the day and cooled by terrestrial vegetation at night, this air often becomes stagnant. As a result, these sheltered sites experience lower nighttime temperatures (especially in winter), higher daytime temperatures (especially in summer), and higher relative humidity. If the temperature drops low enough, frost pockets form in these depressions. The microclimates of the frost pockets often display the same phenomenon, supporting different kinds of plant life than found on surrounding higher ground.

Although the global and regional patterns of climate discussed constrain the large-scale distribution and abundance of plants and animals, the localized patterns of microclimate define the actual environmental conditions sensed by the individual organism. This localized microclimate thus determines the distribution and activities of organisms in a particular region.

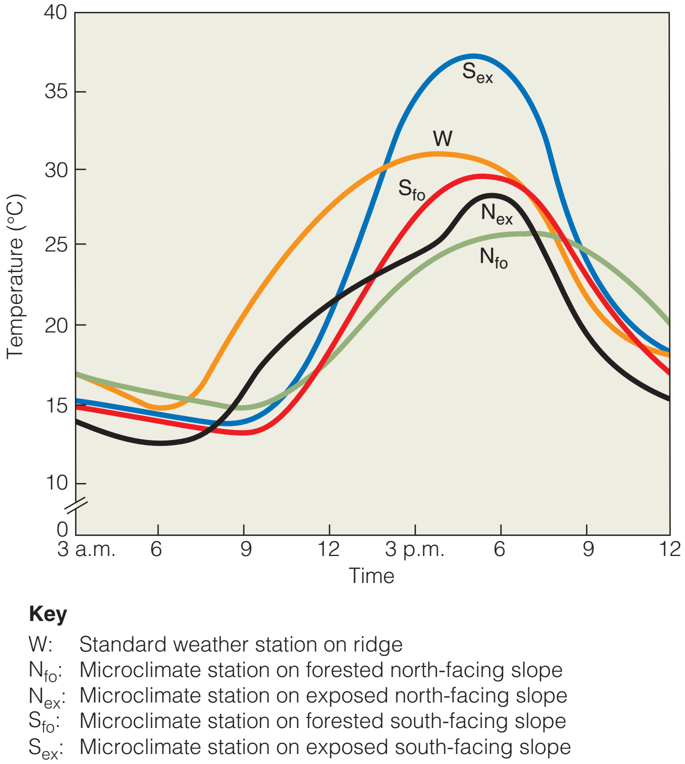


Figure 2.25 Diurnal changes in temperature (single clear day in August) recorded at five weather stations in Greer, West Virginia. Four of the stations provide data on the microclimate of a forested site on north-facing slope position (N_{fo}), an exposed (no vegetation cover) site on north-facing slope position (N_{ex}), a forested site on a south-facing slope (S_{fo}), and an exposed site on a south-facing slope (S_{ex}). The fifth station is located at the standard weather station position on the ridge top.

Interpreting Ecological Data

Q1. *Which of the two slope positions (north- or south-facing) has the higher maximum recorded temperatures (mid-afternoon)?*

Q2. *How does vegetation cover (forested vs. exposed slope) influence surface temperatures?*

ECOLOGICAL Issues & Applications — Rising Atmospheric Concentrations of Greenhouse Gases Are Altering Earth's Climate

Since the middle of the 19th century, direct measurements of surface temperature have been made at widespread locations around the world. These direct measures from instruments such as thermometers are referred to as the *instrumental record*. Besides these measurements made at the land surface, observations of sea surface temperatures have been made from ships since the mid-19th century. Since the late 1970s, both a network of instrumented buoys and Earth-observing satellites have been providing a continuous record of global observations for a wide variety of climate variables, supplementing the previous land- and ship-based instrumental records. What these various sources of data on the land and sea surface temperatures of our planet indicate is that Earth has been warming over the past 150 years (**Figure 2.26**).

Since the early 20th century, the global average surface temperature has increased by 0.74°C (±0.2°C). In addition, the 10 warmest years in the instrumental record since 1850 are, in descending order, 2010, 2005, 1998, 2003, 2013, 2002, 2006, 2009, 2007, and 2004. Analyses also indicate that global ocean heat content has increased significantly since the late 1950s. More than half of the increase in heat content has occurred in the upper 300 meters of the ocean; in this layer the temperature has increased at a rate of about 0.04°C per decade. Additional data examining trends on humidity, sea-ice extent, and snow cover likewise indicate a pattern of warming over the past century. What is the cause of this warming? The scientific consensus is that the warming is in large part a result of rising atmospheric concentrations of greenhouse gases. According to the most recent report of the Intergovernmental Panel on Climate Change (Report of Working Group I, 2013):

> Warming of the climate system is unequivocal, as is now evident from observations of increases in global average air and ocean temperatures.... Most of the observed increase in global average temperatures since the mid-20th century is very likely due to the observed increase in anthropogenic greenhouse gas concentrations.

Although human activities have increased the atmospheric concentration of a variety of greenhouse gases (e.g., methane [CH_4], nitrous oxide [N_2O]), the major concern is focused on carbon dioxide (CO_2). The atmospheric concentration of CO_2 has increased by more than 30 percent over the past 100 years. The evidence for this rise comes primarily from continuous observations of atmospheric CO_2 started in 1958 at Mauna Loa, Hawaii, by Charles Keeling (**Figure 2.27**) and from parallel records around the world. Evidence before the direct observations of 1958 comes from various sources, including the analysis of air bubbles trapped in the ice of glaciers in Greenland and Antarctica.

In reconstructing atmospheric CO_2 concentrations over the past 300 years, we see values that fluctuate between 280 and 290 parts per million (ppm) until the mid-1800s (see Figure 2.27). After the onset of the Industrial Revolution, the value increased steadily, rising exponentially by the mid-19th century onward. The change reflects the combustion of fossil fuels (coal, oil, and gas) as an energy source for industrialized nations (**Figure 2.28a**), as well as the increased clearing and burning of forests (primarily in the tropical regions; see **Figure 2.28b**).

Although there is an obvious correlation between rising atmospheric concentrations of CO_2 (and other greenhouse gases) and the observed increases in global temperature, what makes the scientific community so confident that the observed rise in global temperatures is a result of the greenhouse effect? One important factor is the actual pattern of warming itself. Recall from our discussion of the Earth's radiation balance, that surface temperature at any location or time reflects the net radiation balance, that is, the difference between incoming shortwave radiation and outgoing longwave radiation (Section 2.1). If incoming shortwave radiation exceeds outgoing longwave radiation, surface temperatures rise. Conversely, if outgoing longwave radiation exceeds incoming shortwave radiation, temperatures decline. It is this imbalance that accounts for the decline in mean annual temperatures with increasing latitude from the tropics (net radiation surplus) to the poles (net radiation deficit; see Figure 2.6). Likewise, it is the shift from surplus to deficit that results in the decline in surface temperatures from day to night (diurnal cycle) and from summer to winter (seasonal cycle). Since the influence of greenhouse gases on the radiation balance works through the absorption of outgoing longwave radiation, which is then emitted downward toward the surface instead, the net effect reduces cooling, that is, keeps the surface temperature warmer than it would otherwise be if the longwave radiation were lost to space. It therefore follows that the greater proportional warming from rising levels of greenhouse gases would occur in those places (i.e., polar) and times (i.e., winter and night)

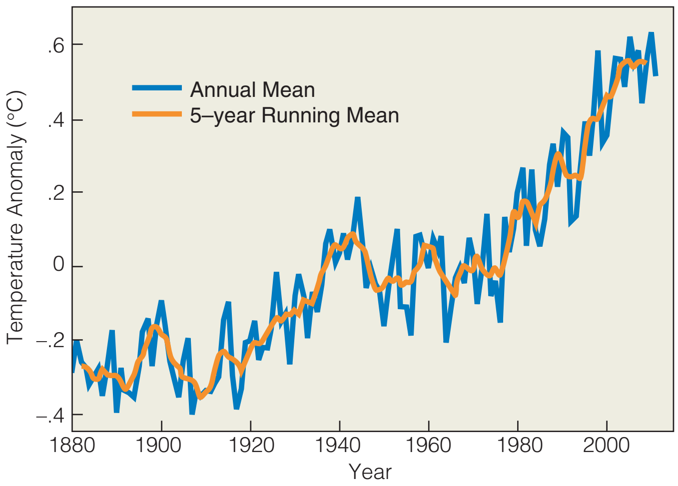


Figure 2.26 Global annual surface temperatures for the period of 1880 to 2012. Temperatures are expressed relative to the 1951 to 1980 mean (temperature anomaly plotted on *y*-axis is annual temperature – mean of annual temperatures over the period from 1951 to 1980). Data are from surface air measurements at meteorological stations and ship and satellite measurements for sea surface temperature. The five-year running mean (red line) is calculated for each year by averaging the sum of that year plus the preceding and following two years.

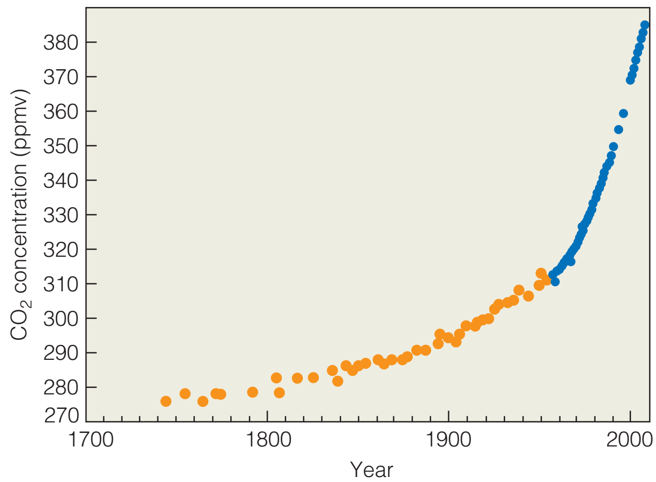
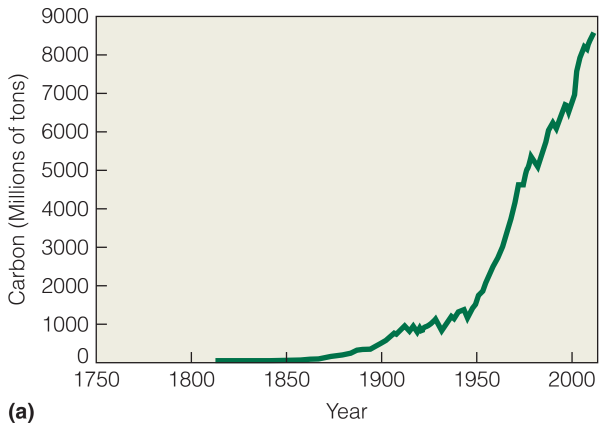


Figure 2.27 Historical record of average atmospheric carbon dioxide (CO_2) concentration over the past 300 years. Data collected prior to direct observation (1958 to present) are estimated from various techniques including analysis of air trapped in Antarctic ice sheets. ppmv, parts per million volume.

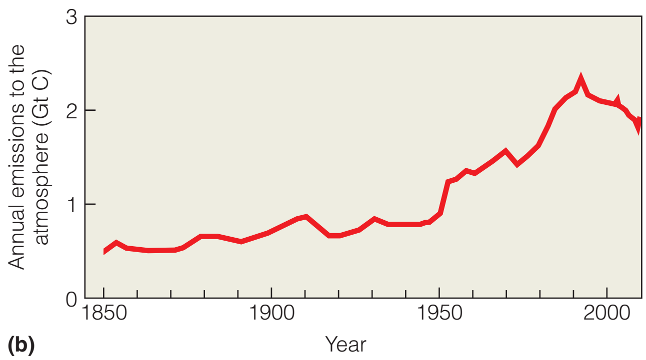
when and where temperatures are generally declining as a result of negative net radiation balance. An analysis of the patterns of warming over the past 50 years is in general agreement with this expectation.

The increase in global mean surface temperature illustrated in Figure 2.27 has not been the same at every location. The global map presented in **Figure 2.29a** shows the geographic patterns of surface temperature changes over the period from 1955 to 2005. Note that the greatest warming has occurred in the polar regions, particularly the Arctic (North America and Eurasia between 40 and 70° N). Although Earth's average temperature has risen 0.74°C during the 20th century, the Arctic is warming twice as fast as other parts of the world. In Alaska (U.S.) average temperatures have increased 3.0°C between 1970 and 2000. The warmer temperatures have caused other changes in the Arctic region such as melting of sea ice and continental ice sheets (Greenland). The reduction in ice cover potentially exacerbates the problem by reducing surface albedo and increasing the absorption of incoming shortwave radiation. In the Southern hemisphere, the Antarctic Peninsula has also undergone a great warming—five times the global average.

The changes in mean surface temperature presented in Figure 2.29a have been partitioned by season (December–February, March–May, June–August, and September–December.) in **Figure 2.29b**. The greatest observed warming over the last half century has occurred during the winter months. In effect, this represents a reduction of the normal pattern of cooling that occurs during the winter months as a result of the deficit in net radiation (deficit is reduced by increased absorption of outgoing longwave radiation). This pattern of

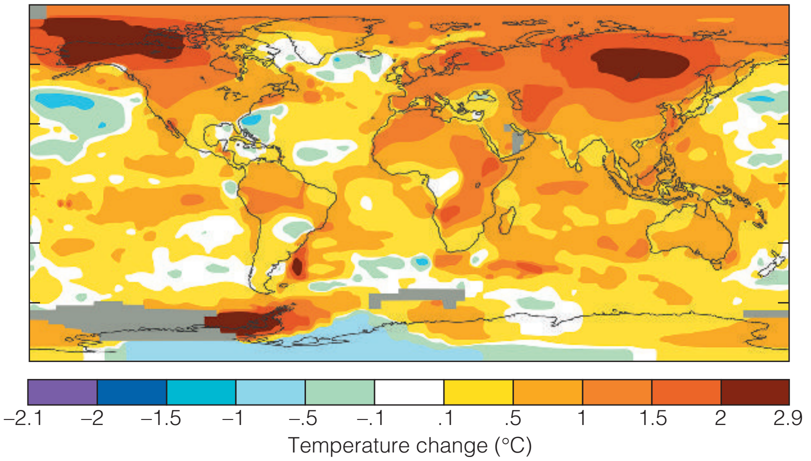


(a)

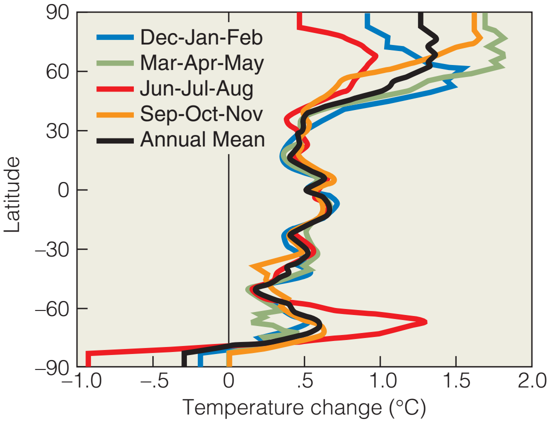


(b)

Figure 2.28 Historical record of global annual input of carbon dioxide (CO_2) to the atmosphere from the burning of fossil fuels since 1750 (a). Historical record of global annual input of CO_2 to the atmosphere from the clearing and burning of forest over the same period (b).
([b] Adapted from Houghton, J. *Global Warming: The Complete Briefing* [Cambridge University Press, 1997].)



(a)



(b)

Figure 2.29 Global map of changes in mean surface temperature over the 50-year period from 1955 to 2005 (a). The changes in mean annual temperature shown in (a) are partitioned by season (December–February, March–May, June–August, and September–December) and averaged by latitude (b).
(NASA Goddard Institute for Space Studies 2005.)

Interpreting Ecological Data

Q1. *Based on the data provided in (b), which latitudes exhibit the greatest seasonal variations in surface temperature (Ts) change?*

Q2. *What accounts for the fact that the period of Jun–Aug in the arctic region (north of 60° N) shows the least warming, while the same period corresponds to the maximum temperature change in the Antarctic (south of 60° S)?*

winter warming becomes more apparent when the seasonal data are analyzed by latitude (see Figure 2.29b). The net result of winter warming is a reduction in the seasonal variations in temperature (differences between the warmest and coldest months).

Analyses of daily maximum and minimum land-surface temperatures from 1950 to 2000 show a decrease in the diurnal temperature range. On average, minimum temperatures are increasing at about twice the rate of maximum temperatures (0.2°C versus 0.1°C per decade). In other words, nighttime temperatures (minimum) have increased more than daytime temperatures (maximum) over this period.

These patterns of increasing surface temperatures over the past century have a major influence on the functioning of ecological systems, arranging the distribution of plant and animal species, the structure of communities, and the patterns of ecosystem productivity and decomposition. We will explore a variety of these issues in the *Ecological Issues & Applications* sections of the chapters that follow, and examine in more detail the current and future implication of global climate change in Chapter 27.

SUMMARY

Net Radiation 2.1

Earth intercepts solar energy in the form of shortwave radiation, some of which is reflected back into space. Earth emits energy back into space in the form of longwave radiation, a portion of which is absorbed by gases in the atmosphere and radiated back to the surface. The difference between incoming shortwave and outgoing longwave radiation is the net radiation. Surface temperatures are a function of net radiation.

Seasonal Variation 2.2

The amount of solar radiation intercepted by Earth varies markedly with latitude. Tropical regions near the equator receive the greatest amount of solar radiation, and high latitudes receive the least. Because Earth tilts on its axis, parts of Earth encounter seasonal differences in solar radiation. These differences give rise to seasonal variations in net radiation and temperature. There is a global gradient in mean annual temperature; it is warmest in the tropics and declines toward the poles.

Atmospheric Circulation 2.3

From the equator to the midlatitudes there is an annual surplus of net radiation, and there is a deficit from the midlatitudes to the poles. This latitudinal gradient of net radiation gives rise to global patterns of atmospheric circulation. The spin of Earth on its axis deflects air and water currents to the right in the Northern Hemisphere and to the left in the Southern Hemisphere. Three cells of global air flow occur in each hemisphere.

Ocean Currents 2.4

The global pattern of winds and the Coriolis effect cause major patterns of ocean currents. Each ocean is dominated by great circular water motions, or gyres. These gyres move clockwise in the Northern Hemisphere and counterclockwise in the Southern Hemisphere.

Atmospheric Moisture 2.5

Atmospheric moisture is measured in terms of relative humidity. The maximum amount of moisture the air can hold at any given temperature is called the saturation vapor pressure, which increases with temperature. Relative humidity is the amount of water in the air, expressed as a percentage of the maximum amount the air could hold at a given temperature.

Precipitation 2.6

Wind, temperature, and ocean currents produce global patterns of precipitation. They account for regions of high precipitation in the tropics and belts of dry climate at approximately 30° N and S latitude.

Continentality 2.7

Land surfaces heat and cool more rapidly than water; as a result, land areas farther from the coast experience a greater seasonal variation in temperature than do coastal areas. The interiors of continents generally receive less precipitation than the coastal regions do.

Topography 2.8

Temperature declines with altitude, so locations at higher elevations will have consistently lower temperatures that those of lower elevations. Mountainous topography influences local and regional patterns of precipitation. As an air mass reaches a mountain, it ascends, cools, becomes saturated with water vapor, and releases much of its moisture at upper altitudes of the windward side.

Irregular Variation 2.9

Not all temporal variation in regional climate occurs at a regular interval. Irregular variations in the trade winds give rise to periods of unusually warm waters off the coast of western South America. Referred to by scientists as El Niño; this phenomenon is a global event arising from large-scale interaction between the ocean and the atmosphere.

Microclimates 2.10

The actual climatic conditions that organisms live in vary considerably within one climate. These local variations, or microclimates, reflect topography, vegetative cover, exposure, and other factors on every scale. Angles of solar radiation cause marked differences between north- and south-facing slopes, whether on mountains, sand dunes, or ant mounds.

Climate Warming Ecological Issues & Applications

Over the past century the average surface temperature of the planet has been rising. The rise in surface temperature is related to increasing atmospheric concentrations of greenhouse gases caused by the burning of fossil fuels and clearing and burning of forests.

STUDY QUESTIONS

1. What is net radiation?
2. What is the greenhouse effect, and how does it influence the net radiation balance (and temperature) of Earth?
3. Why do equatorial regions receive more solar radiation than the polar regions? What is the consequence to latitudinal patterns of temperature?
4. The 23.5° tilt of Earth on its north–south axis gives rise to the seasons (review Figure 2.7). How would the pattern of seasons differ if the Earth's tilt were 90°? How would this influence the diurnal (night–day) cycle?
5. Why are the coastal waters of the southeastern United States warmer than the coastal waters off the southwestern coast? (Assume the same latitude. Hint: Look at the direction of the prevailing surface currents presented in Figure 2.13.)
6. The air temperature at noon on January 20 was 45°F, and the air temperature at noon on July 20 at the same location was 85°F. The relative humidity on both days was 75 percent. On which of these two days was there more water vapor in the air?
7. How might the relative humidity of a parcel of air change as it moves up the side of a mountain? Why?
8. What is the Intertropical Convergence Zone (ITCZ), and why does it give rise to a distinct pattern of seasonality in precipitation in the tropical zone?
9. What feature of global atmospheric circulation gives rise to the desert zones of the midlatitudes?
10. Which aspect of a slope, south- or north-facing, would receive the most solar radiation in the mountain ranges of the Southern Hemisphere?
11. Spruce Knob (latitude 38.625° N) in eastern West Virginia is named for the spruce trees dominating the forests at this site. Spruce trees are typically found in the colder forests of the more northern latitudes (northeastern United States and Canada). What does the presence of spruce trees at Spruce Knob tell you about this site?

FURTHER READINGS

Classic Studies

Geiger, R. 1965. *Climate near the ground*. Cambridge, MA: Harvard University Press.
A classic book on microclimate that continues to be a major reference on the subject.

Current Research

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An excellent introductory text on climate, clearly written and well illustrated.

Fagen, B. 2001. *The Little Ice Age*: *How climate made history*, *1300–1850*. New York: Basic Books.
An enjoyable book that gives an overview of the effects of the Little Ice Age on human history.

Graedel, T. E., and P. J. Crutzen. 1997. *Atmosphere*, *climate and change*. New York: Scientific American Library.
A short introduction to climate written for the general public. Provides an excellent background for those interested in topics relating to air pollution and climate change.

Philander, G. 1989. "El Niño and La Niña." *American Scientist* 77:451–459.

Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor and H. L. Miller (eds.). 2007. *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. UK: Cambridge University Press.
The most recent report of the IPCC outlining the state of the science regarding the issue of global climate change.

Suplee, C. 1999. "El Niño, La Niña." *National Geographic* 195:73–95.
These two articles provide a general introduction to the El Niño–La Niña climate cycle.

CHAPTER 3

The Aquatic Environment

A rainstorm over the ocean—a part of the water cycle.

CHAPTER GUIDE

WATER IS THE ESSENTIAL SUBSTANCE OF LIFE, the dominant component of all living organisms. About 75–95 percent of the weight of all living cells is water, and there is hardly a physiological process in which water is not fundamentally important.

Covering some 75 percent of the planet's surface, water is also the dominant environment on Earth. A major feature influencing the adaptations of organisms that inhabit aquatic environments is water salinity (see Section 3.5). For this reason, aquatic ecosystems are divided into two major categories: saltwater (or marine) and freshwater. These two major categories are further divided into a variety of aquatic ecosystems based on the depth and flow of water, substrate, and the type of organisms (typically plants) that dominate. We will explore the diversity of aquatic environments and the organisms that inhabit them later (Chapter 24). For now, we will examine the unique physical and chemical characteristics of water and how those characteristics interact to define the different aquatic environments and constrain the evolution of organisms that inhabit them.

3.1 Water Cycles between Earth and the Atmosphere

All marine and freshwater aquatic environments are linked, either directly or indirectly, as components of the **water cycle** (also referred to as the **hydrologic cycle**; **Figure 3.1**)—the process by which water travels in a sequence from the air to Earth and returns to the atmosphere.

Solar radiation, which heats Earth's atmosphere and provides energy for the evaporation of water, is the driving force behind the water cycle (see Chapter 2). **Precipitation** sets the water cycle in motion. Water vapor, circulating in the atmosphere, eventually falls in some form of precipitation. Some of the water falls directly on the soil and bodies of water. Some is intercepted by vegetation, dead organic matter on the ground, and urban structures and streets in a process known as **interception**.

Because of interception, which can be considerable, various amounts of water never infiltrate the ground but evaporate directly back to the atmosphere. Precipitation that reaches the soil moves into the ground by **infiltration**. The rate of infiltration depends on the type of soil, slope, vegetation, and intensity of the precipitation (see Section 4.8). During heavy rains when the soil is saturated, excess water flows across the surface of the ground as **surface runoff** or overland flow. At places, it concentrates into depressions and gullies, and the flow changes from sheet to channelized flow—a process that can be observed on city streets as water moves across the pavement into gutters. Because of low infiltration, runoff from urban areas might be as much as 85 percent of the precipitation.

Some water entering the soil seeps down to an impervious layer of clay or rock to collect as **groundwater** (see Figure 3.1). From there, water finds its way into springs and streams. Streams coalesce into rivers as they follow the topography of the landscape. In basins and floodplains, lakes and wetlands form. Rivers eventually flow to the coast, forming the transition from freshwater to marine environments.

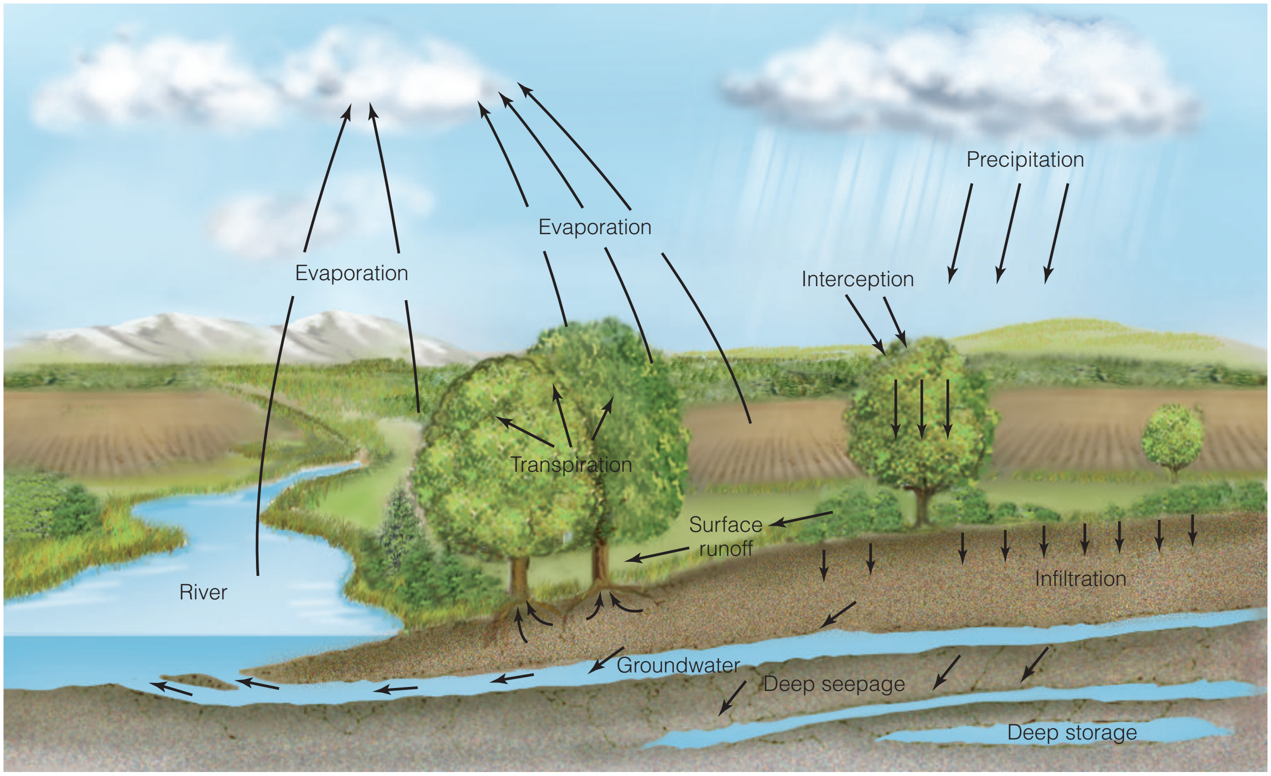

Figure 3.1 The water cycle on a local scale, showing major pathways of water movement.

Water remaining on the surface of the ground, in the upper layers of the soil, and collected on the surface of vegetation—as well as water in the surface layers of streams, lakes, and oceans—returns to the atmosphere by evaporation. The rate of evaporation is governed by how much water vapor is in the air relative to the saturation vapor pressure (relative humidity; see Section 2.5). Plants cause additional water loss from the soil. Through their roots, they take in water from the soil and lose it through their leaves and other organs in a process called transpiration. **Transpiration** is the evaporation of water from internal surfaces of leaves, stems, and other living parts (see Chapter 6). The total amount of evaporating water from the surfaces of the ground and vegetation (surface evaporation plus transpiration) is called **evapotranspiration**.

Figure 3.2 is a diagram of the global water cycle showing the various reservoirs (bodies of water) and fluxes (exchanges between reservoirs). The total volume of water on Earth is approximately 1.4 billion cubic kilometers (km^3) of which more than 97 percent resides in the oceans. Another 2 percent of the total is found in the polar ice caps and glaciers, and the third-largest active reservoir is groundwater (0.3 percent). Over the oceans, evaporation exceeds precipitation by some 40,000 km^3. A significant proportion of the water evaporated from the oceans is transported by winds over the land surface in the form of water vapor, where it is deposited as precipitation. Of the 111,000 km^3 of water that falls as precipitation on the land surface, only some 71,000 km^3 is returned to the atmosphere as evapotranspiration. The remaining 40,000 km^3 is carried as runoff by rivers and eventually returns to the oceans. This amount balances the net loss of water from the oceans to the atmosphere through evaporation that is eventually deposited on the continents (land surface) as precipitation (see Figure 3.2).

The relatively small size of the atmospheric reservoir (only 13 km^3) does not reflect its importance in the global water cycle. In Figure 3.2, note the large fluxes between the atmosphere, the oceans, and the land surface relative to the amount of water residing in the atmosphere at any given time (e.g., the size of atmospheric reservoir). The importance of the atmosphere in the global water cycle is better reflected by the turnover time of this reservoir. The turnover time is calculated by dividing the size of the reservoir by the rate of output (flux out). For example, the turnover time for the ocean is the size of the reservoir (1.37×10^6 km^3) divided by the rate of evaporation (425 km^3 per year) or more than 3000 years. In contrast, the turnover time of the atmospheric reservoir is approximately 0.024 year. That is to say, the entire water content of the atmosphere is replaced on average every nine days.

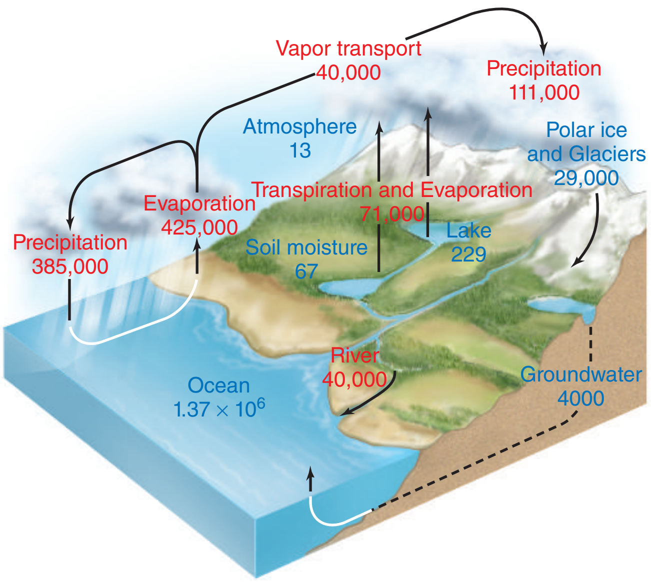

Figure 3.2 Global water cycle. Values for reservoirs (shown in blue) are in 10^8 km^3. Values for fluxes (shown in red) are in km^3 per year.

3.2 Water Has Important Physical Properties

The physical arrangement of its component molecules makes water a unique substance. A molecule of water consists of two atoms of hydrogen (H) joined to one atom of oxygen (O), represented by the chemical symbol H_2O. The H atoms are bonded to the O atom asymmetrically, such that the two H atoms are at one end of the molecule and the O atom is at the other (**Figure 3.3a**). The bonding between the two hydrogen atoms and the oxygen atom is via shared electrons (called a *covalent bond*), so that each H atom shares a single electron with the oxygen. The shared hydrogen atoms are closer to the oxygen atom than they are to each other. As a result, the side of the water molecule where the H atoms are located has a positive charge, and the opposite side where the oxygen atom is located has a negative charge, thus polarizing the water molecule (termed a *polar covalent bond*; **Figure 3.3b**).

Because of its polarity, each water molecule becomes weakly bonded with its neighboring molecules (**Figure 3.3c**). The positive (hydrogen) end of one molecule attracts the negative (oxygen) end of the other. The angle between the hydrogen atoms encourages an open, tetrahedral arrangement of water molecules. This situation, wherein hydrogen atoms act as connecting links between water molecules, is called **hydrogen bonding**. The simultaneous bonding of a hydrogen atom to the oxygen atoms of two different water molecules gives rise to a lattice arrangement of molecules (**Figure 3.3d**). These bonds, however, are weak in comparison to the bond between the hydrogen and oxygen atoms. As a result, they are easily broken and reformed.

Water has some unique properties related to its hydrogen bonds. One property is high **specific heat**—the number of calories necessary to raise the temperature of 1 gram of water 1 degree Celsius. The specific heat of water is defined as a value of 1, and other substances are given a value relative to that of water. Water can store tremendous quantities of heat energy with a small rise in temperature. As a result, great quantities of heat must be absorbed before the temperature of natural waters, such as ponds, lakes, and seas, rises just 1°C. These waters warm up slowly in spring and cool off just as slowly in the fall. This process prevents the wide seasonal fluctuations in the temperature of aquatic habitats so characteristic of