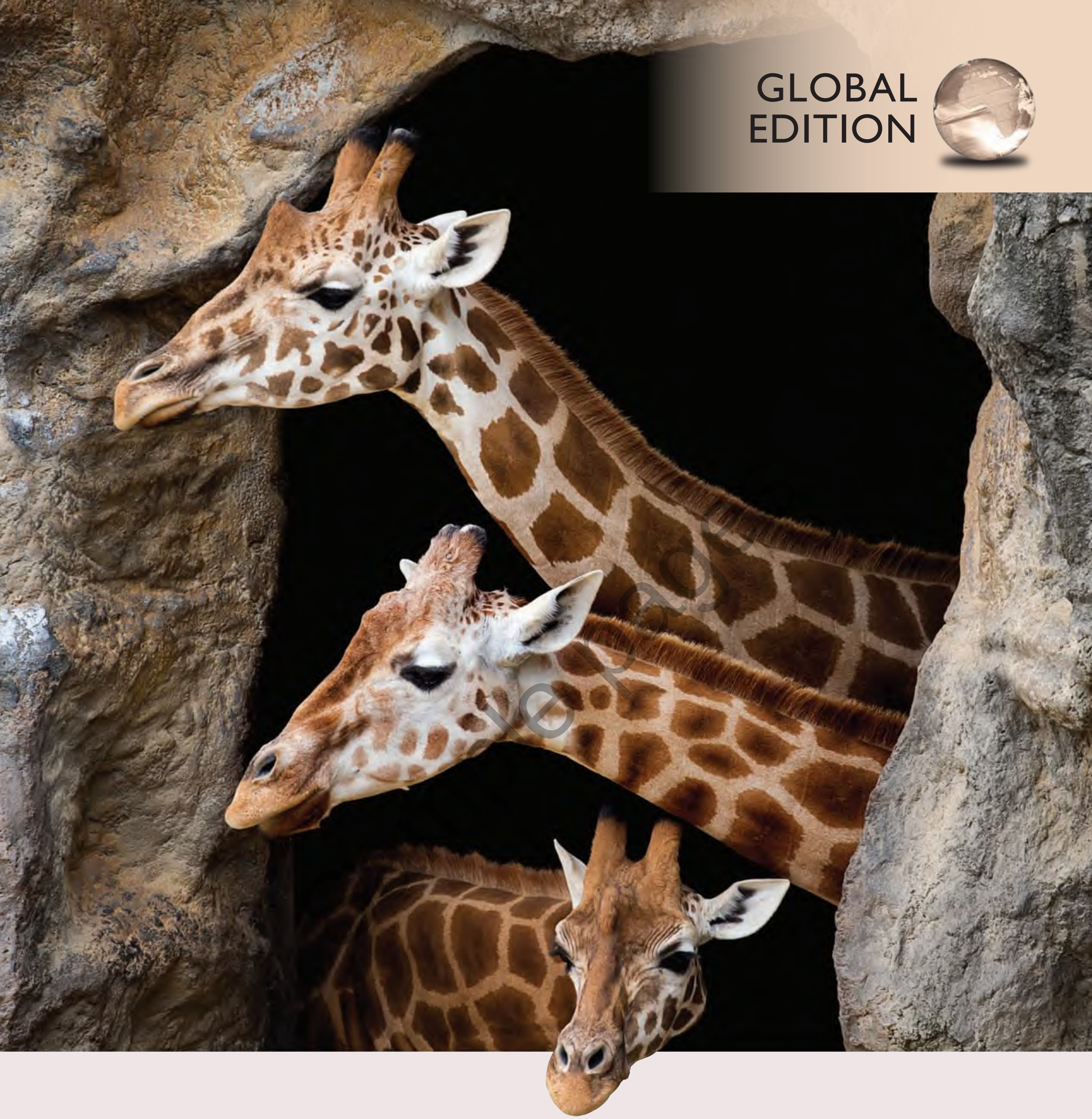

GLOBAL EDITION

Elements of ECOLOGY

NINTH EDITION

Thomas M. Smith • Robert Leo Smith

ALWAYS LEARNING

PEARSON

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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.

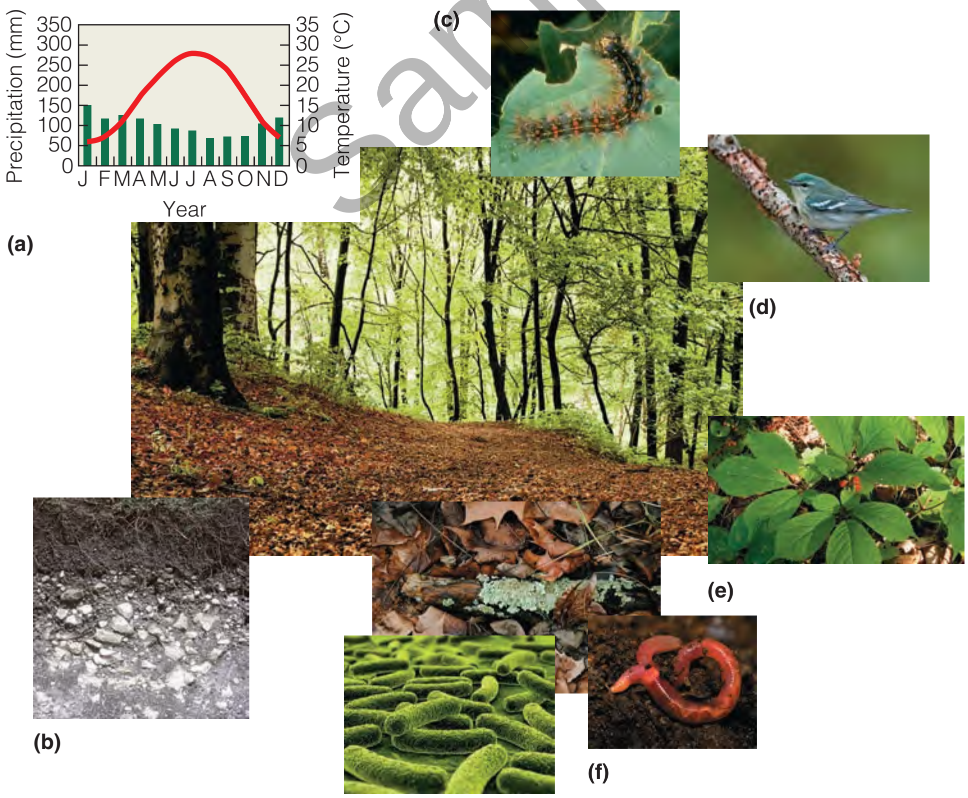
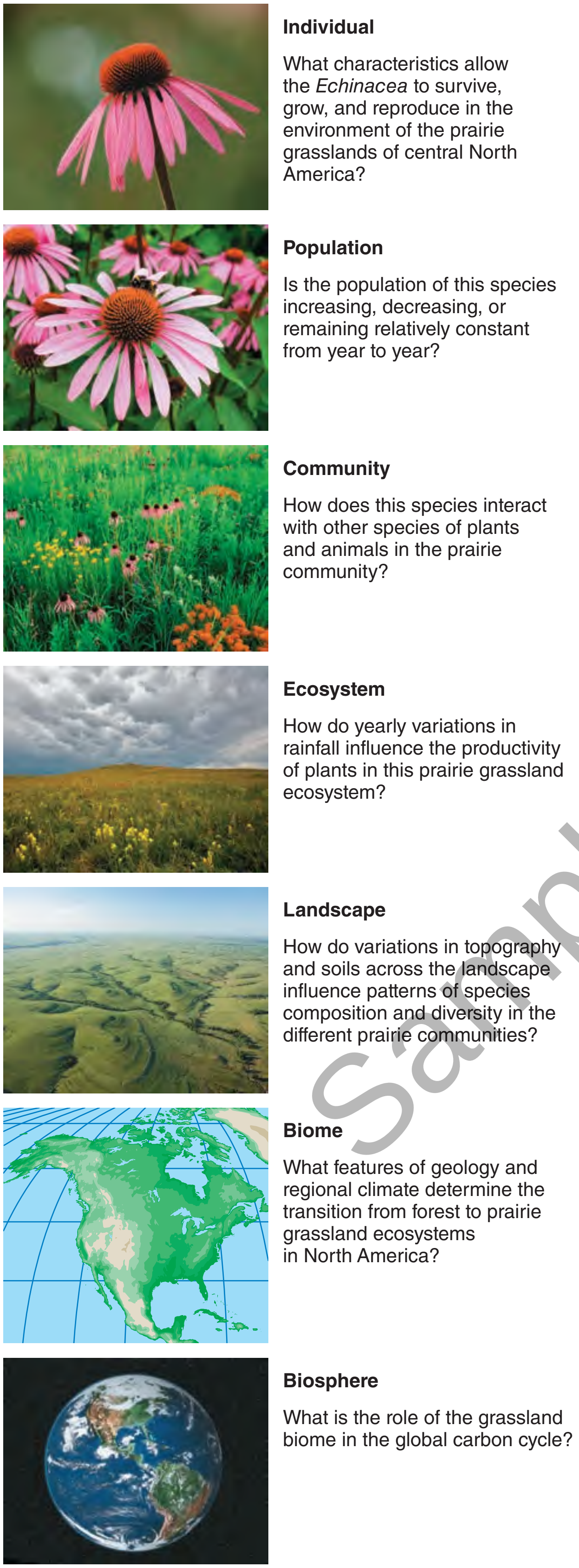


Figure 1.2 Example of the components and interactions that define a forest ecosystem. The abiotic components of the ecosystem, including the (a) climate and (b) soil, directly influence the forest trees. (c) Herbivores feed on the canopy, (d) while predators such as this warbler feed upon insects. (e)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

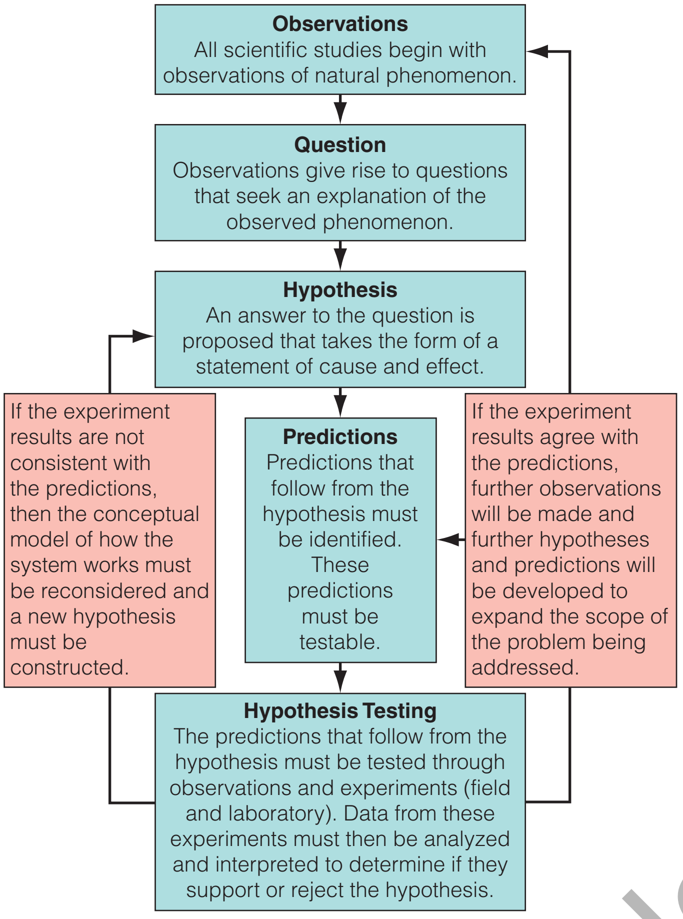


Figure 1.4 A simple representation of the scientific method.

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

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

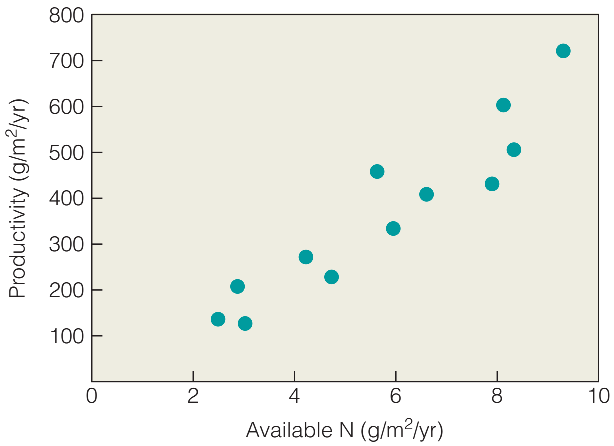


Figure 1.5 The response of grassland production to soil nitrogen availability. Nitrogen (N), the independent variable, is plotted on the *x*-axis; grassland productivity, the dependent variable, is plotted on the *y*-axis.

Interpreting Ecological Data

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

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

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

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

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

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.

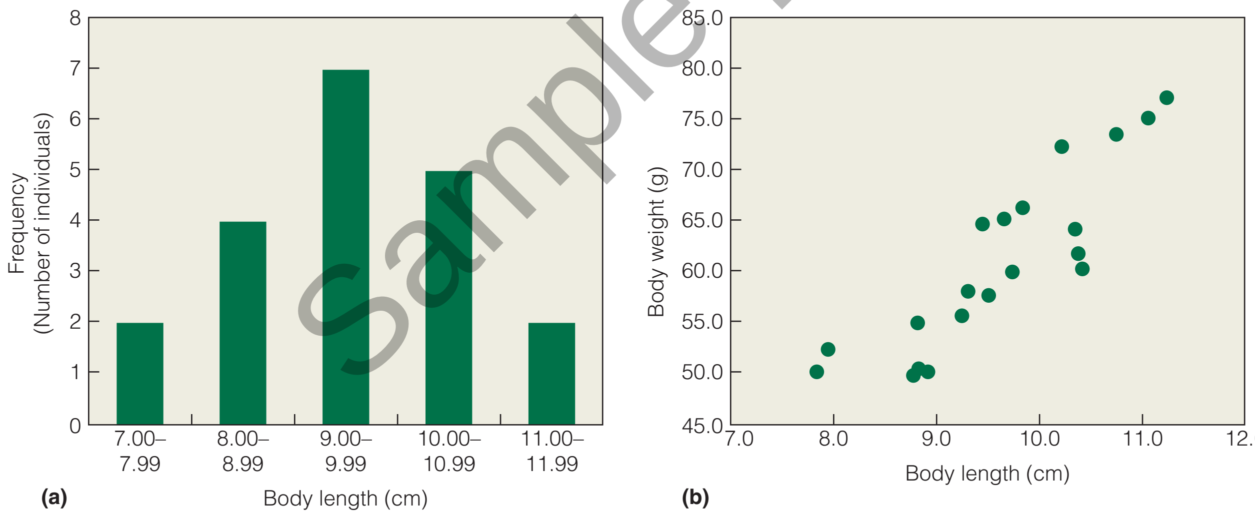


Figure 1 (a) An example of a histogram relating the number of individuals belonging to different categories of body length from a sample of the sunfish population. (b) Scatter plot relating body length (*x*-axis) and body weight (*y*-axis) for the sample of sunfish presented in (a).

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)?

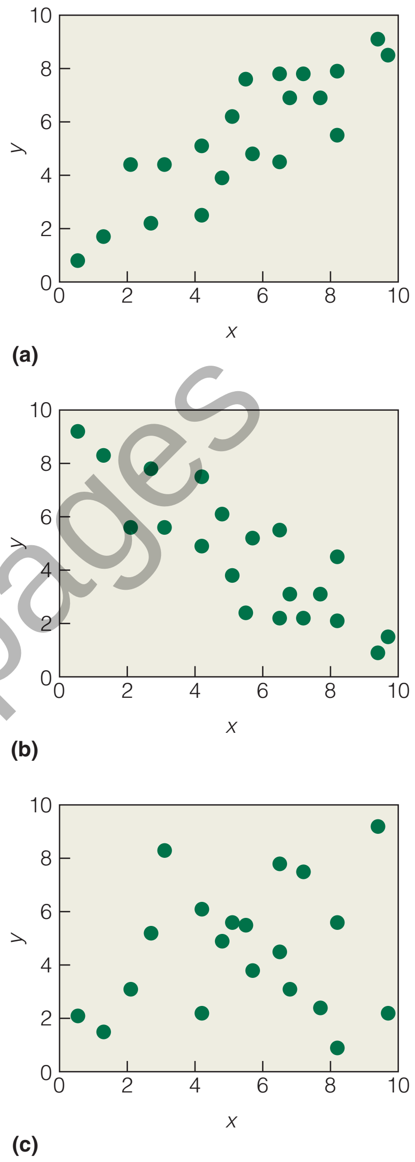


Figure 2 Three general patterns for scatter plots.

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

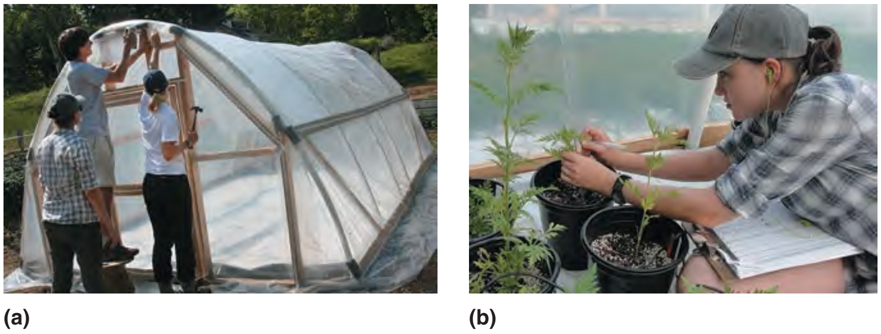


Figure 1.7 (a) Undergraduate research students at Harvard Forest erect temporary greenhouses that were used to create different carbon dioxide (CO_2) treatments for a series of experiments directed at testing the response of ragweed (*Ambrosia artemisiifolia*) to elevated atmospheric CO_2. (b) Response 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.

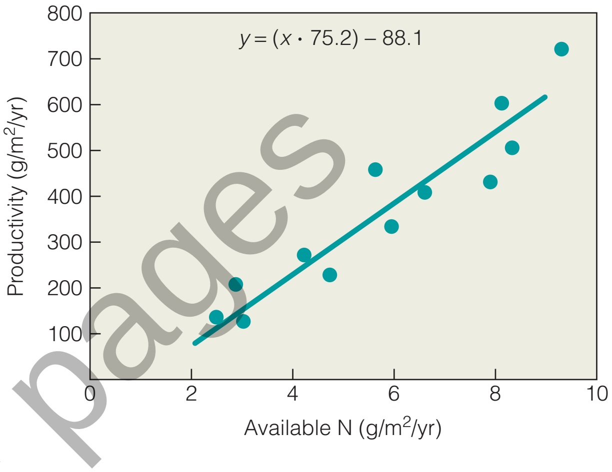


Figure 1.8 A simple linear regression model to predict grassland productivity (*y*-axis) from nitrogen availability (*x*-axis). The general form of the equation is $y = (x \times b) + a$, where b is the slope of the line (75.2) and a is the y-intercept (–88.1), or the value of y where the line intersects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

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 39 for the first example.)

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. What is the ultimate goal of all living organisms? What role does the ecosystem play in every organism's life?
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 the scientific method? Describe the steps involved in it.
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.