CHAPTER

1

Introduction to Ecosystem Science

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Humans have devised many intellectual systems to understand and manage the complicated world in which we live, from physics to philosophy to economics. In this book, we present one such intellectual system, ecosystem science, which tries to make sense of the complex natural world and helps us manage it better. As we will see, ecosystems can be highly varied in size and character, from a little pool of water in a tree cavity, to a redwood forest, to a neighborhood in a city, to a frigid river, to the entire globe (Figure 1.1). Nevertheless, a common set of tools and ideas can be used to analyze and understand these varied and complicated systems. The results of these analyses are both intellectually satisfying and useful in managing our planet for the benefit of nature and humankind. Indeed, because of the growing demands placed on living and nonliving resources by humans, it has been argued that ecosystem science is one of the essential core disciplines needed to understand and manage the modern planet Earth (Weathers et al. 2016).

This book defines the ecosystem, illustrates the ecosystem approach, describes the chief characteristics of ecosystems and the major tools that scientists use to analyze them, and presents important discoveries that scientists have made about ecosystems. It also lays out some critical questions for the future. Although the book is not focused on the management of ecosystems, several management implications of ecosystem science are described and illustrated.

What Is an Ecosystem?

An ecosystem is the interacting system made up of all the living and nonliving objects in a specified volume of space.

This deceptively simple definition both says much and leaves out much. First, as with other systems (Box 1.1), ecosystems contain more than one object, and those objects interact. More

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FIGURE 1.1 Some examples of ecosystems: (A) the frigid Salmon River, Idaho; (B) a residential neighborhood in Baltimore, Maryland; (C) a biofilm on a rock in a stream; (D) a section of the southern ocean containing a phytoplankton bloom; (E) a redwood forest in the fog in California; (F) a tree cavity; (G) the Earth. (Photocredits: A—John Davis; B—Baltimore Ecosystem Study LTER; C—Colden Baxter; D—US government, public domain; E—Samuel M. Simkin; F—Ian Walker; G—Source: https://www.publicdomainpictures.net/en/view-image.php?image=86448&picture=planet-earth.)

surprisingly, living and nonliving objects are given equal status in ecosystem science. A particle of clay and the plant drawing its nutrition from that clay particle are both parts of an ecosystem, and therefore equally valid objects of study. This viewpoint contrasts with physiology and population ecology, for example, in which the organism is the object of study,

BOX 1.1

Some Nonecological Systems

Thinking about some of the many familiar examples of nonecological systems may help you understand how ecosystems are described and compared. A system is just a collection of two or more interacting objects. A few familiar systems include the group of planets rotating around the sun as a system (the solar system); the group of electrons, protons, and neutrons forming an atom; and the system of banks that controls the money supply of the United States (the Federal Reserve System). Just as with ecosystems, we can describe these systems by their structures, their functions, and the factors that control them.

A description of system structure often begins with the number and kinds of objects in the system. Thus, we might note that our solar system contains eight or nine planets; or that the copper atom has 29 electrons, 29 protons, and 35 neutrons; or that the Federal Reserve System contains a seven-member Board of Governors, 12 banks, and 26 branch banks. Systems have functional properties as well—the copper atom exchanges electrons with other atoms in chemical reactions, and the Federal Reserve System exchanges money with other banks. Systems may be described according to their controls as well. Gravity and rotational dynamics control the motions of the planets, and the copper atom is controlled by strong and weak atomic forces, whereas the Federal Reserve System is controlled by the decisions of its Board of Governors (who, in turn, are chosen by a president who is elected by the voters of the United States). All of these descriptions allow us to understand how each system works. Perhaps more importantly, they let us compare one system to another—our solar system with those of other stars; the copper atom with the cadmium atom; the current banking system in the United States with that of France, or with that of the United States in the 19th century. Ecosystem scientists likewise describe ecosystems in various ways to understand them better, and to allow comparisons across ecosystems.

Systems science, the general field of understanding all kinds of systems, is well developed. Many of the conceptual frameworks for ecosystem science are those of system science (e.g., Hogan and Weathers 2003; Mobus and Kalton 2015).

and the nonliving environment is conceived of as an external influence on the object of study. Finally, the definition implies that ecosystems have definite boundaries, but does not tell us how we might go about setting or finding the boundaries to an ecosystem.

There are some unexpectedly powerful advantages to this simple definition. First, by including all living and nonliving objects in a specified space, it is possible to use the tool of mass balance to follow the movement and fate of materials (Box 1.2). Material that comes into an ecosystem must either stay in the ecosystem or leave—there is no other possible fate for the material. Mass balance offers a convenient quantitative tool for measuring the integrated activity of entire, complicated systems without having to measure the properties and interactions of each of its parts. It also allows ecosystem scientists to estimate the size of a single unknown flux by difference. Consequently, it will become evident throughout the book that ecosystem scientists often use the powerful tool of mass balance.

BOX 1.2

Ecosystem Goods and Services

Ecosystems provide many valuable goods and services to people. People have recognized for a long time that ecosystems provide physical, marketable products such as timber and fish, and have often managed ecosystems to protect or increase the supply of these goods. As economics and ecology have developed, it has become apparent that ecosystems provide many things other than marketable goods that are of value to people. For instance, ecosystems may remove pollutants, reducing the cost of providing drinking water or clean air to breathe. They may protect us from diseases, or protect our infrastructure from flooding. People may get peace of mind, write songs (Coscieme 2015), or even heal faster (Ulrich 1984) when they have access to natural ecosystems.

One commonly used framework for enumerating and organizing these diverse benefits (Millennium Ecosystem Assessment 2003, 2005) organizes the benefits that ecosystems provide to people into four broad classes (Table 1.1). We offer several observations about this list (or indeed any list of ecosystem services). First, the list of goods and services that ecosystems provide to people is long and varied, ranging from tangible goods sold on the open market to the least tangible of benefits, and including everything from physical and biogeochemical characteristics of ecosystems to specific parts of specific plants and animals. Attempts to put a dollar value on these services often result in very large estimates. For example, a famous early analysis by Costanza et al. (1997) estimated the global value of ecosystem services to be USD $16–54 *trillion*/year. Second, some of these ecosystem services are easy to quantify and value in dollars, whereas others are more elusive. Thus, it seems easy to place a value on X board feet of oak timber sold on the open market in the year 2015 for Y dollars, but how does one quantify the spiritual satisfaction that arises from contemplating a flowing river? Nevertheless, economists have developed methods to estimate the value of even the most elusive of ecosystem services (EPA Science Advisory Board 2009). Third, it is a fundamental and serious mistake to assume that ecosystem services that are hard to quantify are trivially small, and can be left out of analyses. For instance, cultural ecosystem services typically are difficult to quantify, and so are often omitted from estimates of ecosystem services. Yet Carson et al. (2003) estimated that the existence value associated with the Exxon Valdez oil spill in Prince William Sound was at least USD $2.8 billion (in 1990 dollars), for example. Fourth, if we are to use an ecosystem services framework to guide the management of ecosystems and aid in environmental decision-making so that aggregate ecosystem benefits to humans are maximized, then it is essential to include all kinds of ecosystem services in the analysis. It's easy to see that deciding whether to build a dam by considering only the hydroelectricity to be generated, but not the effects of the dam on navigation, fisheries, or recreation, is likely to lead to a poor decision. Similarly, considering any subset of ecosystem services instead of the entire array of services is likely to result in a decision that does not maximize benefits to people. Finally, many ecologists object to any attempt at reducing the value of nature to a dollar value, considering it inappropriate.

Continued

BOX 1.2 (*cont'd*)

TABLE 1.1 Categories of ecosystem services.

Type of Service	Examples
Provisioning	Provision of food, fresh water, wood, fiber, and biochemicals such as natural medicines directly to humans
Regulating	Regulation of climate, air quality, diseases, erosion, or natural hazards such as floods; pollination
Cultural	Provision of recreational, aesthetic, religious, spiritual, or educational opportunities to people
Supporting	Where an ecosystem provides structures or functions that support any of the other three classes of services; examples include soil formation and nutrient cycling

Modified from Millennium Ecosystem Assessment (2003, 2005) and Costanza et al. 2017.

Second, defining an ecosystem as we have done makes it possible to measure the total activity of an ecosystem without having to measure all the parts and exchanges within the ecosystem. This advantage is sometimes referred to as a "black-box" approach, because we can measure the function (input and output) of a box (the ecosystem) without having to know what is in the box (Figure 1.2). Sometimes ecologists debate whether it is philosophically possible to predict the properties of a complex system by studying its parts (reductionism) or whether it is necessary to study intact systems (holism). It is not necessary to accept the philosophical claims of holism, though, to recognize that studies of whole systems may be a much more efficient way than reductionism to understand ecosystems. Such a holistic approach to ecosystems is a powerful tool of ecosystem science, and is often combined with reductionist approaches to develop insights into the functioning and controls of ecosystems.

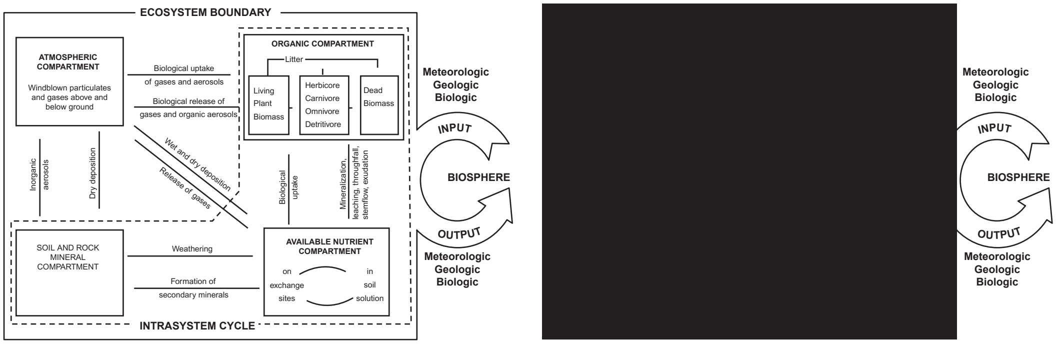

FIGURE 1.2 Two views of the same ecosystem. The *left side* shows some of the parts inside an ecosystem and how they are connected, as well as the exchanges between the ecosystem and its surroundings, whereas the *right side* shows a black-box approach in which the functions of an ecosystem (i.e., its inputs and outputs) can be studied without knowing what is inside the box. (Modified from Likens 1992.)

Third, the definition gives the investigator complete flexibility in choosing where to set the boundaries of the ecosystem in time and space. The boundaries of an ecosystem (i.e., size, location, and timescale) can therefore be chosen to match the question that the scientist is trying to answer. Boundaries often are drawn at places where fluxes are easy to measure (e.g., a single point on a stream as it leaves a forested, watershed-ecosystem) or so that fluxes across the boundary are small compared to cycling inside the ecosystem (e.g., a lake shore). Nevertheless, boundaries are required to make quantitative measures of these fluxes. It is true that ecosystems frequently are defined to be large (e.g., lakes and watersheds that are hectares to square kilometers in size) and are studied on the scale of days to a few years, but there is nothing in the definition of an ecosystem that *requires* ecosystems to be defined at this scale. Indeed, as we will see, an ecosystem may be as small as a single rock or as large as the entire Earth (see Chapter 7), and can be studied for time periods as long as hundreds of millions of years.

Fourth, defining an ecosystem to contain both living and nonliving objects recognizes the importance of both living and nonliving parts of ecosystems in controlling the functions and responses of these systems. There are examples throughout the book in which living organisms, nonliving objects, or both acting together determine what ecosystems look like (structure) and how they work (function). Furthermore, the close ties and strong interactions between the living and nonliving parts of ecosystems are so varied and so strong that it would be very inconvenient if not misleading to study one without the other. Thus, the inclusion of living and nonliving objects in ecosystems has practical as well as intellectual advantages.

Finally, we note one further property of ecosystems: they are open to the flow of energy and materials. It might be theoretically possible to define particular examples of ecosystems that are closed systems, not exchanging energy or materials with their surroundings, but nearly all ecosystems as actually defined have important exchanges of energy and materials with their surroundings. Indeed, such exchanges are one of the central subjects of ecosystem science. We note in particular that most ecosystems depend on energy inputs from external sources, either as energy from the sun or as organic matter brought in from neighboring ecosystems.

Now consider briefly what is missing from the definition. We have already noted that the definition does not specify the time or space scales over which an ecosystem is defined, or where exactly the boundaries are placed. Ecosystems are not required to be self-regulating, permanent, stable, or sustainable. They are not required to have any particular functional properties. For example, they need not be in balance or efficient in the way that they process materials. Our definition does not require ecosystems to have a purpose. Although ecosystems change over time, the basic definition does not suggest anything about the nature or direction of that change. It might seem like a shame not to include such interesting attributes in a definition of ecosystem (O'Neill 2001), and indeed some ecologists have incorporated such attributes in their definitions, but we think it is neither necessary nor helpful to include them in a basic definition. They may, however, be useful hypotheses and the subject of fruitful research projects. For instance, we might hypothesize that as forest ecosystems recover from disturbances like fire or clear-cutting, they retain a higher proportion of nutrient inputs from precipitation or release from weathering substrates. This viewpoint is quite different than saying that ecosystems *are* systems that tend to maximize efficiency of use of limiting nutrients.

What Are the Properties of Ecosystems?

All systems have characteristic properties that allow us to describe them and compare them with other similar systems (Box 1.1). How might we describe the properties of ecosystems?

What Is in an Ecosystem?

We might begin simply by listing the contents of an ecosystem. Plants and animals occur in most ecosystems. As we will see later in the book, the number and kinds of plants and animals can have a strong influence on ecosystem function. Many ecosystems also contain people. Historically, many ecologists treated humans as outside of the ecosystem, or deliberately studied ecosystems without people, but it is now common to treat people and our institutions as parts of ecosystems (e.g., Pickett et al. 2001, 2011; McPhearson et al. 2016). Certainly the structure and function (and change) of many modern ecosystems cannot be understood without considering human activities.

Almost all ecosystems contain microbes (bacteria and fungi); although these are not as conspicuous as plants and animals, their activities are vital to ecosystem functioning. Viruses occur in most ecosystems, and may play important roles as regulators of plant, animal, and microbial populations. Ecosystems also contain water and air, which are themselves resources for many organisms and also serve as media in which organisms and nonliving materials can be transported, both within and across the boundaries of ecosystems. Finally, ecosystems contain an enormous variety of nonliving materials, organic and inorganic, solid and dissolved. These nonliving materials, including such disparate items as dead wood, clay particles, bedrock, oxygen, and dissolved nutrients, interact with the living biota and exercise strong influences on the character and functioning of ecosystems. Thus, the total inventory of an ecosystem can be very long; it might contain thousands or millions of kinds of items, living and nonliving, and countless numbers of individuals in these "kinds."

Ecosystems Have Structure

This complexity allows for an essentially infinite number of possible descriptions of ecosystem structure. Nevertheless, only a few descriptions of ecosystem structure are commonly used by the scientists who study ecosystems. Often ecosystems are described by the numbers and kinds of objects that they contain, focusing on key materials or organisms. Thus, we may describe an ecosystem as having a plant biomass of 300 g/m^2, or a deer population of $5/km^2$, or a nitrogen content of 200 kg/ha. Sometimes ecosystem scientists describe ecosystems by the ratios of key elements such as the nitrogen:phosphorus ratio of a lake ecosystem. If we were interested in the role of biological communities in regulating ecosystem function, we would refer to the biodiversity (especially the species richness) of the organisms in the ecosystem. We may be interested in the spatial variation, as well as the mean value, of any such key variables (see Chapter 11). Thus, we may describe ecosystems as being highly patchy as opposed to relatively homogeneous in nitrogen content or biodiversity. Finally, scientists often describe ecosystems by their size or location (e.g., latitude, altitude, biogeographic realm, or distance from the coast).

Ecosystems Perform Functions

In the broadest sense, ecosystems consume energy and transform materials. As with all systems subject to the second law of thermodynamics, some of the useful energy that comes into ecosystems (crossing the ecosystem's boundary) in forms such as solar radiation, chemical energy (e.g., organic matter), or mechanical energy (e.g., wind) is degraded to heat and becomes unable to perform further work. In particular, living organisms need a continual source of energy to maintain biochemical and physiological integrity, as well as to perform activities such as swimming, running, or flying. Curiously, although these biological energy transformations are only a part of the energy transformations that occur in an ecosystem, most studies of energy flow through ecosystems treat only forms of energy that can be captured and used by living organisms (i.e., solar radiation and chemical energy), and ignore purely abiotic processes such as the conversion of kinetic energy to heat by flowing water. Organisms can capture solar energy or chemical energy from inorganic compounds (photosynthesis and chemosynthesis, respectively), store energy, obtain energy from other organisms (e.g., predation), or convert energy into heat (respiration). Patterns of energy flow through ecosystems can be of direct interest to humans who harvest wild populations, and can tell ecosystem scientists a good deal about how different ecosystems function.

Ecosystems also transform materials in various ways. Materials that come into the ecosystem may be taken up by some part of the ecosystem and accumulate. In some cases, this accumulation may be temporary so that the ecosystem acts as a sort of capacitor, releasing the material at a later time. The lag time between atmospheric deposition of sulfate onto a terrestrial ecosystem and its export in stream water from that system is an example. Ecosystems may also be a source of material, releasing their internal stores to neighboring systems. Methane gas flux from a wetland to the atmosphere is an example. Finally, and perhaps most interesting, ecosystems transform materials by changing their chemical and physical states (Chapter 6). Nitric acid contained in rainwater falling on a forest soil may react with the soil and form calcium nitrate in soil water. The nitrate in the solution may then be taken up by a plant and incorporated into protein in a leaf. At the end of the growing season, the leaf may fall into a stream where it is eaten by an insect and chopped into small leafy bits, which then wash out of the ecosystem. The description of chemical and biological transformations by ecosystems forms the field of biogeochemistry (e.g., Schlesinger and Bernhardt 2013; see Chapter 7), which is a major part of modern ecosystem science (and this book). Many biogeochemical functions are important to humans (e.g., the removal of nitrate by riparian forests in the Mississippi River basin; see Chapter 19, Figure 19.2), as well as essential to understanding how different ecosystems work.

Ecosystems often are described by their functions as well as their structures. One of the most common functional descriptions of ecosystems is whether the system is a source or a sink of a given material—that is, whether the inputs of that material to the ecosystem are less or more, respectively, than the outputs of that material from the ecosystem. In the special case of energy flow through ecosystems, the degree to which an ecosystem is a source or a sink is described by the P/R (gross photosynthesis to respiration) ratio for the system. At a steady state, ecosystems with a P/R ratio less than 1 must import chemical energy (usually organic matter) from neighboring ecosystems and are called heterotrophic; those with a P/R ratio greater than 1 export chemical energy to neighboring ecosystems and are called autotrophic. Another useful functional description is the residence time of a given material in an ecosystem—that is, the average amount of time that a material spends within an ecosystem. Residence time is calculated by dividing the standing stock of the material in the ecosystem by its input rate.

Ecosystem structures and functions can have economic value. For instance, ecosystems provide lumber, they purify water and air, they regulate the prevalence of human diseases, and they provide pollination for crop plants. These and many other goods and services provided by ecosystems are commonly called "ecosystem services"—the benefits that people derive from ecosystem structures and functions (e.g., Daily 1997; Millennium Ecosystem Assessment 2005; Kareiva et al. 2011, Box 1.2). Developing ways to estimate quantitatively the value of ecosystem services is an important and growing field at the intersection of ecology, sustainability science, and economics.

Ecosystem Structure and Function Are Controlled by Many Factors

Unlike systems such as the solar system, the dynamics of which are controlled by just a few factors, ecosystem structure and function depend on many factors. Ecosystem scientists have learned much about how ecosystems are controlled, and much of the remainder of this book will be concerned with this subject. Ecosystem structure and function often are affected by organisms (including humans), either through trophic activities such as herbivory, predation, and decomposition, or through engineering activities (Jones et al. 1994) such as burrowing, shelter construction (e.g., beaver dams), and the like (see Box 12.1 in Chapter 12). Likewise, the nonliving parts of ecosystems often control ecosystems by determining supplies and movement of air, water, key nutrients, and other materials. Temperature is another abiotic factor that has strong effects on ecosystems. Finally, because most ecosystems are open and exchange energy and materials with the ecosystems that surround them or that preceded them, the structure and function of an ecosystem can be strongly affected by its spatial and temporal context.

Ecosystems Change Through Time

Ecosystems change through time (see Chapters 11 and 12). These changes may be gradual and subtle (the millennial releases of nutrients from a weathering soil) or fast and dramatic (a fire sweeping through a forest). Both external forces (changes in climate or nutrient inputs) and internal dynamics (aging of a tree population, accumulation or depletion of materials in a soil or a lake) are important in driving temporal changes in ecosystems. In some cases, changes are directional and predictable (e.g., soil weathering, the filling of a lake basin), while in other cases changes may be idiosyncratic and difficult to predict (e.g., the arrival of an invasive species, disturbance by a hurricane). Understanding and predicting how ecosystems change through time is of great theoretical and practical interest, and is a major part of contemporary ecosystem science.

How Do We Classify or Compare Ecosystems?

Thus, ecosystem scientists use structure, function, control, and temporal dynamics to classify and compare ecosystems. For instance, it is common to see ecosystems described as rich in nitrogen (structure), sinks for carbon (function), fire-dominated (control), or recently disturbed (dynamics). All of these attributes of ecosystems can provide useful frameworks to classify ecosystems, and ultimately to organize and interpret the vast amount of information that scientists have collected about ecosystems. Similar descriptions and classifications are evident throughout the book.

Why Do Scientists Study Ecosystems?

Scientists have been motivated to study ecosystems for several reasons. To begin with, if ecosystems truly are the "basic units of nature" on Earth (Tansley 1935), any attempt to understand our planet and the products of evolution on it must include ecosystem science as a central theme. Indeed much study of ecosystem science has been motivated by simple curiosity about how our world and how systems—whether ecological, social, or socio-ecological—work. Many salable products such as timber and fish are taken directly from "wild" ecosystems, so many early ecosystem studies were carried out to try to understand better the processes that supported these products and ultimately increase their yields. Especially in the past 30 years, we have come to realize that the valuable products of nature include far more than obviously salable products like timber and fish. Ecosystems also provide us with clean air and water, opportunities for recreation and spiritual fulfillment, protection from diseases, and many more "ecosystem services" (Box 1.2). Human economies and well-being are wholly embedded in and dependent on wild ecosystems. Thus, many contemporary ecosystem studies are concerned with how ecosystems provide this broad array of services, how human activities reduce or restore the ability of ecosystems to provide these services, and ultimately how to reconcile the growing demands of human populations with the needs of both nature and ourselves for functioning ecosystems.

How Do Ecosystem Scientists Learn about Ecosystems?

Depending on the problem that they are studying, ecosystem scientists use a wide variety of approaches and an array of simple to sophisticated tools to measure different aspects of ecosystem structure and function. We offer a few examples here; however, new approaches and tools emerge every year, and with them come more ways to open black boxes in ecosystem science (see Chapter 19).

Approaches for Learning about Ecosystems

There are multiple approaches by which scientists can understand ecosystem structure, function, and development, both qualitatively and quantitatively. Five approaches (modified from the lists of Likens 1992; Carpenter 1998) are especially important in ecosystem science,

TABLE 1.2 Strengths and limitations of approaches to understanding ecosystems. Natural history observations and understanding underpin all of these approaches.

Approach	Some Strengths	Some Limitations
Theory	Flexibility of scale; integration; deduction of testable ideas	Cannot develop without linkage to observation and experiment
Long-term observation	Temporal context; detection of trends and surprises; test hypotheses about temporal variation	Potentially site-specific; difficult to determine cause; costly and difficult to maintain
Comparison	Spatial or interecosystem context; detection of spatial pattern; test hypotheses about spatial variation	Difficult to predict temporal change or response to perturbation
Ecosystem experiment	Measure ecosystem response to perturbation; test hypothesis about controls and management of ecosystem processes	Potentially site-specific; potentially difficult to rule out some explanations; hard to do; expensive

After Carpenter (1998).

including: (1) natural history or observation; (2) theory and conceptual models; (3) long-term study; (4) cross-ecosystem comparison; and (5) experiments. These approaches are complementary to one another (Table 1.2), and are best used in combination. Almost every scientific question of any complexity or importance in ecosystem science requires the use of two or more of these approaches to get a robust answer.

Natural History

A good deal can be learned about ecosystems simply from watching them and documenting what is observed in some fashion. Do fallen leaves decay in place, wash away into a stream, or burn in episodic fires? Is the soil deep and rich, or shallow and rocky? Does it freeze in the winter? As a result, our understanding of an ecosystem often is based on simple observations of its natural history. Indeed, without such careful observations, even the most sophisticated studies can go astray by formulating nonsensical questions or omitting key observations or measurements. Not surprisingly, careful natural history studies (such as Forbes' "The Lake as a Microcosm," discussed later) were important precursors to modern ecosystem science. Although these forerunners of ecosystem science often included speculation about ecosystem processes, they did not have the technical means to measure easily such functions as net ecosystem productivity or nutrient cycling, or to quantify trophic transfers.

Long-Term Studies

Long-term studies (i.e., those lasting for more than 10 years—longer than the tenure of most grants or the time it takes to earn a PhD!) are relatively rare in ecology as a whole (Lindenmayer and Likens 2018). However, long-term studies are especially good at providing insight into slow processes (e.g., changes associated with forest succession), subtle changes (e.g., changing chemistry of precipitation), rare events (e.g., the coldest winter, effects of hurricanes or insect outbreaks), or processes controlled by multiple interacting factors (e.g., fish recruitment; Likens 1989; Lindenmayer and Likens 2018; and see the Long-Term Ecological Research Program (LTER) of the National Science Foundation, http://www.lternet.edu). Sometimes long-term understanding can be obtained by short-term analyses of materials that record history, such as soil or sediment cores, otoliths (fish ear-stones), or written historical records. For example, analysis of pollen, diatoms, pigments, or geochemistry in lake sediment can reveal the millennium-long history of terrestrial vegetation, phytoplankton, soils, and lake level—in short, the history of the development of the linkages between terrestrial and aquatic ecosystems. It is from long-term studies or their surrogates that scientists have documented climatic, atmospheric, geochemical, and organismal changes over decades to billions of years.

Cross-Ecosystem Comparison

Comparative studies have served two important roles in ecosystem science. Most simply, scientists often have measured some variable associated with ecosystem structure or function across a series of ecosystems to identify typical values of that variable, show how it varies among types of ecosystems, and generate hypotheses about what factors might control that variable. An example of such an analysis is shown in Table 2.1 in Chapter 2. Alternatively, scientists often test whether some factor controls an ecosystem by comparing ecosystems that differ in that factor and not (to the extent possible) in any other relevant characteristic. For instance, if we wanted to test whether phosphorus inputs control primary production in lakes, we might try to measure primary production in a series of 10 lakes of similar size, depth, species composition, and terrain that differ in their phosphorus inputs. In practice, it often is difficult to find such a perfect series of well-matched ecosystems that could serve as study sites.

Experiments

Experiments, whether conducted in the laboratory or in the field, are powerful ways to reveal controls on ecosystem structure and function (Likens 1985; Weathers et al. 2016). There are no rules about the size of experimental units: manipulations have been made across hundreds of square kilometers (e.g., iron fertilization experiments conducted in the ocean) and within square centimeters. Often, the goal of experiments is to measure an ecosystem's response to a change in a single variable while holding all others as constant as possible. For example, to understand whether phytoplankton in lakes were controlled by phosphorus or by other nutrients such as nitrogen and carbon, scientists in the Experimental Lakes Area of Canada added phosphorus, nitrogen, and carbon to one-half of a lake (cut in two by a massive curtain) and just nitrogen and carbon to the other half. They then compared responses—such as the amount of primary production—in each half of the lake to see the effects of the treatments. This whole-lake experiment helped to demonstrate that phosphorus was a major factor controlling algal productivity in the lakes being tested (but see Chapter 9).

Theory and Conceptual Models

As in other sciences, ecosystem scientists routinely use theory and conceptual models. Such theories and models are highly varied in structure and purpose (Canham et al. 2003; Pickett et al. 2007; Childers et al. 2014). Models may be as simple as a statistical regression (see Chapter 12) or a box-and-arrow diagram drawn on a napkin, or as complex as a detailed

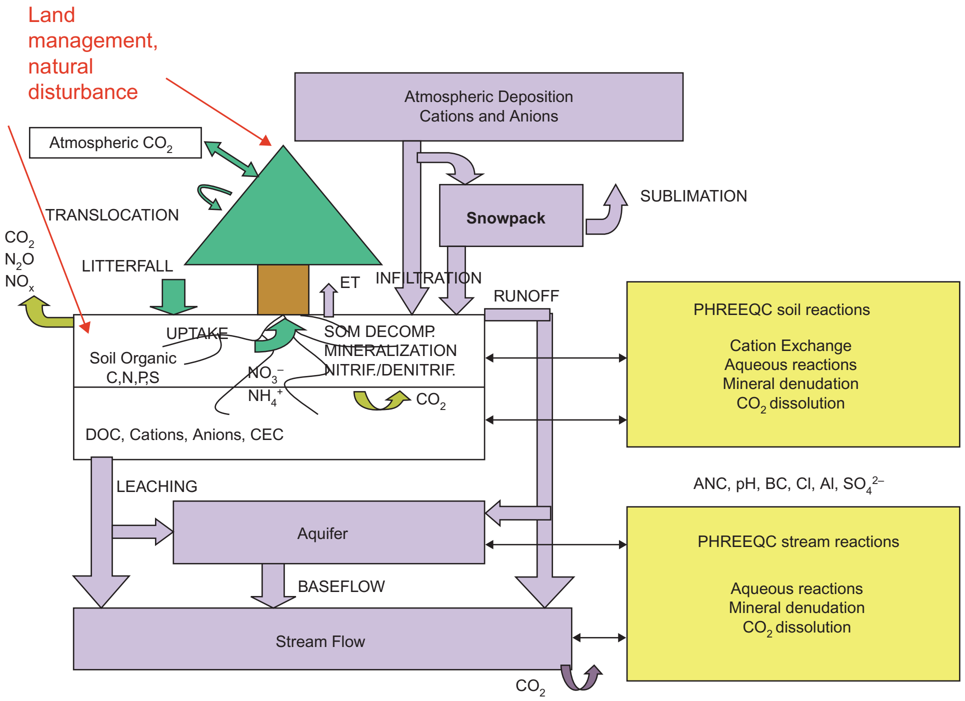

FIGURE 1.3 DayCent-Chem model processes. DayCent-Chem was developed to address ecosystem responses to combined atmospheric nitrogen and sulfur deposition. DayCent-Chem operates on a daily time step and computes atmospheric deposition, soil water fluxes, snowpack and stream dynamics, plant production and uptake, soil organic matter decomposition, mineralization, nitrification, and denitrification *(left side of figure)* while utilizing PHREEQC's (an aqueous geochemical equilibrium model) low-temperature aqueous geochemical equilibrium calculations, including CO_2 dissolution, mineral denudation, and cation exchange, to compute soil water and stream chemistry *(right side of figure)*, *ANC*, acid neutralizing capacity; *BC*, base cations (Ca, Mg, K, Na); *CEC*, cation exchange capacity; *DOC*, dissolved organic carbon; and evapotranspiration; *ET*, evapotranspiration. The model requires considerable site-specific environmental data to run. (From Hartman et al. 2009, Figure 1.3.)

simulation model (Figure 1.3). Models are highly flexible, can cover scales of time and space that are difficult to study using other approaches, and often can provide quick answers at low cost. They also are very useful as a way to organize facts and ideas, to generate, sharpen, or narrow hypotheses, and to guide research activities. Scientists often make rapid progress by tightly coupling theory and models to other approaches.

What Do Ecosystem Scientists Measure?

Ecosystem scientists are inherently interested in the connections between structure and function of ecosystems, and how these develop over time. Thus, many of the examples of measurements or values in this book are related to structure and function, such as biomass of a species, or rates of carbon cycling. They are what is often found on the x or y axes of graphs, or are used as treatments or are measured as responses in experiments. Ecosystem structure is sometimes measured by variables such as leaf area index or the number of trophic levels in a lake (see Chapter 11). Productivity (Chapters 2 and 3), rates of decomposition (Chapter 4) or mineralization (Chapter 7) over time or space, or the accumulation of some element of interest can be indicators of ecosystem function. Ecosystem development is often described by changes in structure, function, and their relationship over time (e.g., linked changes in soil and vegetation over millennia).

Many, if not most, of our measurements of ecosystem function are indirect. Sometimes we can measure function directly, such as gas exchange, but these measurements are almost inevitably made on a tiny fraction of the ecosystem (e.g., individual leaves within a grassland or bottle of water from a lake). To estimate a flux over a larger area of a grassland, for example, an ecosystem scientist might deploy eddy covariance instruments that measure carbon dioxide, water, temperature, and wind speed and direction continuously at a place within the grassland (see Chapter 2). From these measures, a model can be used to infer carbon dioxide flux into or out of the ecosystem.

Scientists often choose indirect measures because they are easier to obtain across larger parts of a system or across more systems. As another example, the measurement of chlorophyll-*a* is often used as an indicator of primary productivity in aquatic ecosystems. However, chlorophyll-*a* is not a direct measure of productivity, but a measure of the presence of a pigment used in photosynthesis, and the photosynthetic process builds biomass. Likewise, the carbon:nitrogen (C:N) ratio in soil is often used as an indicator of litter or soil quality, and is used to predict decomposition rates, or rates of nitrogen cycling (see Chapters 4 and 8). To make these indirect measures useful, empirical relationships between direct and surrogate measures must be established—quantifying these relationships is an active area of research.

Some Tools in the Ecosystem Scientist's Toolbox

Ecosystem scientists try to answer a diverse range of questions about a wide array of characteristics of the most varied kinds of ecosystems, using many scientific approaches. It will therefore come as no surprise that ecosystem scientists use an enormous number of specific scientific techniques in their investigations, some simple, some sophisticated, some developed within the discipline, and some borrowed and adapted from other disciplines. These techniques are far too numerous to list and discuss here. Nonetheless, several tools are worth introducing because they are characteristic of ecosystem science and will appear repeatedly in the coming chapters; some exciting, emerging tools are noted in the last chapter.

Balances: Mass and Charge

Mass balance (Box 1.3) is a major tool in ecosystem science, especially for ecosystems in which the boundaries are defined by their watersheds. Mass balances are how all ecosystems are connected: outputs from one system are inputs for another. The First Law of Thermodynamics tells us that matter and energy are not created or destroyed. When both inputs and outputs of energy or matter can be measured relatively completely and accurately, it is possible to construct a mass balance and infer processes. For example, a watershed analysis that does not balance (quantitatively) suggests that either the element of interest is being retained in (inputs > outputs) or leaking from (outputs > inputs) the ecosystem (see Chapters 6 and 10). The watershed mass balance approach was pioneered in the 1960s by

BOX 1.3

Mass Balance

To see just how useful the tool of mass balance can be, suppose we are trying to evaluate whether a lake ecosystem is taking up or releasing phosphorus. We could try to measure all the exchanges between parts of the ecosystem (e.g., the uptake of phosphorus by phytoplankton and rooted plants; the consumption and excretion of phosphorus by the animals that eat phytoplankton and plants; the release of phosphorus during the decay of phytoplankton, plants, and animals; and dozens of other exchanges), then simply sum up all of these measurements. It would take an enormous amount of work to measure all the exchanges, and our final answer would be fraught with large uncertainties. Alternatively, we could define a lake ecosystem that was bounded by the lake shore, the overlying air, and the bedrock deep beneath the lake sediments. Using mass balance, we note that the amount of phosphorus being retained by the lake ecosystem is simply the amount of phosphorus going into the lake minus the amount that is leaving the lake. Now we just have to measure the exchanges across the ecosystem boundary (stream water and groundwater going into and out of the lake; rain, snow, and particles falling on the lake; and any animals entering and leaving the lake—hard enough!) to calculate whether the lake is taking up or releasing phosphorus. In the case of Mirror Lake, New Hampshire (Figure 1.4), almost 40% of incoming phosphorus is retained by the lake.

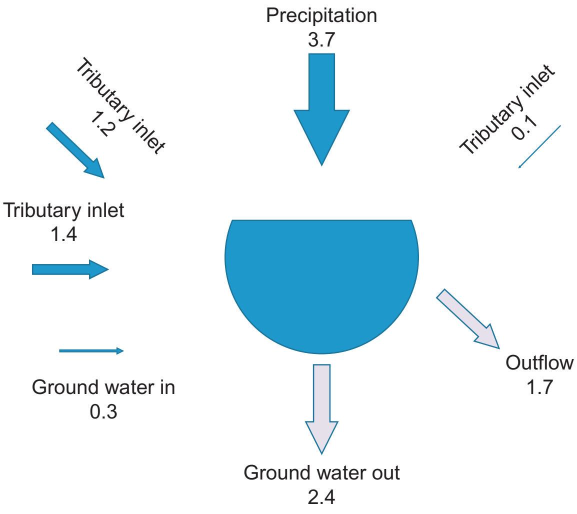

FIGURE 1.4 Average phosphorus inputs and outputs in kilograms/year to Mirror Lake, NH. Total average inputs = 6.7 kg/year; total average outputs = 4.1 kg/year. Inputs − outputs = 2.7 kg/year or 39.7% retention of phosphorus in the lake. (Data from Winter and Likens 2009.)

scientists at the Hubbard Brook Experimental Forest, New Hampshire (Bormann and Likens 1967; Likens 2013), and has been used powerfully around the world to understand the abiotic and biotic movement of a suite of elements through ecosystems.

The other powerful "balance" tool that ecosystem scientists use is *charge balance*. In water, the charges held by positive ions (cations) and negative ions (anions) must balance each other. That is, for every anion (such as chloride) in an aqueous solution, there must be a corresponding cation (such as sodium). Why is this tool so useful? Charge balance tells us, for example, that when an anion moves through a forest soil from groundwater into a stream, it must be accompanied by a corresponding cation (see Chapter 6). The sum of all the negative charges brought by anions must be balanced by the same number of positive charges from cations. Charge balance also makes it possible to check whether the major ions in a water sample have been measured correctly; a charge imbalance tells us that a measurement error has been made or that we have not quantified all the cations or anions that are important in a sample.

Tracers

As useful as balances are as tools, they tell us about the bulk (or net) movements of materials through ecosystems, and rarely allow us to distinguish among different pathways of material movement within ecosystems. All nitrogen atoms look alike to a mass balance. Tracers are tools that allow ecosystem scientists to distinguish among particular pathways of material movement by labeling just some of the atoms or molecules of interest. Ecosystem scientists have used several tracer methods, which have been enormously powerful in understanding how ecosystems work.

Radioisotopes (Box 1.4) were some of the first tracers used in ecosystem science. Radioisotopes can be detected and quantified at very low concentrations, so they make excellent tracers, and have had many applications in ecosystem science. In the mid-20th century, ecosystem scientists added small amounts of radioisotopes to ecosystems to trace the movement of water and the uptake and movement of carbon and limiting nutrients, such as phosphorus, through ecosystems. Radioisotopes are no longer added to natural ecosystems as tracers because of associated health risks, but they continue to be used widely in laboratory studies and measurements (e.g., to measure microbial production; see Chapter 3). They also are used in "natural abundance" studies where ecosystem scientists use the very low natural abundance of radioisotopes to trace the movement of materials through ecosystems, rather than adding radioisotopes to ecosystems. For example, Caraco and her colleagues (2010) observed that the concentration of ^{14}C in organic matter that washed into the Hudson River from the soils of its watershed was very different than that of organic matter produced by photosynthesis within the river. They could therefore use ^{14}C to trace movement of terrestrial organic matter through the Hudson River food web, and show that modern zooplankton were being supported in part by carbon that was captured by primary production thousands of years ago (Figure 1.5).

Stable isotopes have largely taken the place of radioisotopes as tracers outside the laboratory (Box 1.4). Although much more difficult to measure and often expensive to use, stable isotopes do not present a health risk to humans and wildlife. Stable isotopes are available for many elements of ecological interest, including hydrogen, nitrogen, carbon, oxygen, and sulfur. Stable isotopes often are added to ecosystems (or to laboratory experiments) and followed as they move through the system. For example, Templer and her colleagues

BOX 1.4

Ecological Tracers: Isotopes

Most elements exist in several forms that contain different numbers of neutrons (but the same number of protons and electrons, and basically the same chemical properties). For example, about 99% of the carbon on Earth is ^{12}C, which contains six protons, six electrons, and six neutrons, but about 1% of the carbon is ^{13}C, which contains seven neutrons. A tiny amount (~0.0000000001%) of the carbon is ^{14}C, which has eight neutrons. Some isotopes are stable, while others are radioactive (i.e., they spontaneously decay into other elements or isotopes). In the case of carbon, ^{12}C and ^{13}C are stable isotopes, whereas ^{14}C is a radioisotope that decays into nitrogen (^{14}N) with a half-life of 5730 years. Some isotopes that commonly make an appearance in ecosystem science include the radioisotopes ^{3}H (tritium), ^{14}C, ^{32}P, and ^{35}S, and the stable isotopes ^{2}H (deuterium), ^{13}C, ^{15}N, ^{18}O, and ^{34}S, although many other isotopes have been used in specialized studies.

The concentration of stable isotopes is usually expressed in a "del" (δ) notation that compares the abundance of the heavier isotope to that of the lighter isotope.

Thus, the abundance of ^{13}C in a sample is expressed as:

$$\delta^{13}C(‰) = \left(\frac{\left(^{13}C^{12}C\right)_{\text{sample}}}{\left(^{13}C^{12}C\right)_{\text{standard}}} - 1 \right) \times 1000$$

The standard in this case is Vienna Pee Dee Belemnite (a particular kind of fossil). Negative δ values indicate that the heavier isotope is less abundant in the sample than in the standard, while positive δ values indicate that the heavier isotope is more abundant in the sample than in the standard.

(2005) added a stable isotope of nitrogen, ^{15}N, to forest plots in the Catskill Mountains, NY, and then followed it into soil, microbial biomass, understory plants, tree roots, wood, and leaves, and found that most of the nitrogen stayed in the soil. Alternatively, ecosystem scientists often use natural abundance studies of stable isotopes to follow the movement of materials through ecosystems.

Substances other than isotopes can be used as tracers as well. For instance, certain fatty acids cannot be synthesized by animals and are made only by particular kinds of algae. By analyzing the fatty acid content of zooplankton and fish, the contribution of different kinds of algae throughout the food web can be traced. Caffeine, which is not readily degraded in conventional sewage treatment plants, is sometimes used as a tracer for sewage. The kinds of substances that can be used as tracers are highly varied, limited only by the ingenuity and analytical capabilities of the investigator.

Spatial Data

Where are the regions of high and low productivity around the globe? How do they change over the seasons? These are questions that can now be answered largely as a result of the availability of remote sensing tools and spatially explicit data. The ability to collect, represent, and analyze spatially explicit data has risen exponentially over the past decade (Weathers

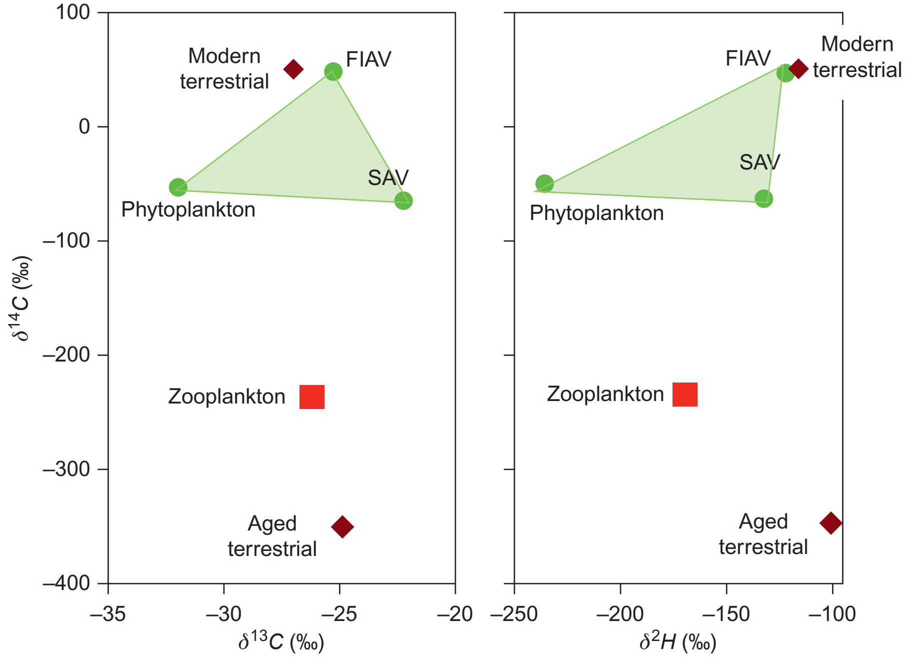

FIGURE 1.5 Use of stable and radioisotopes to determine the source of organic matter supporting zooplankton in the Hudson River. Isotope bi-plots show ^{14}C vs. ^{13}C *(left side)* and ^{14}C vs. ^{2}H *(right side)*. Sources of carbon from modern primary production are shown near the tops of the graphs (*FlAV*, floating-leaved aquatic vegetation; *SAV*, submersed aquatic vegetation). If zooplankton were composed of carbon and hydrogen from these sources, then the data for isotopic composition of zooplankton would fall in the same region of the graph as the sources. Instead, zooplankton fall far outside this region of the graph, showing that they must be composed of organic matter from both modern and "aged" sources (i.e., organic matter thousands of years old from the soils of the Hudson River's watershed). *(From* Caraco et al. 2010.*)*

et al. 2016). Remote sensing and the georeferencing of basic data on landscape characteristics such as elevation, water bodies, land cover, and geological materials have opened the door to a description of ecosystem structure over large areas (see Holmes and Likens 2016; Boucher et al., 2018). Geographic information systems (GISs) allow analysis of the relationships between these structures and fluxes in or out of these systems. For example, the variation in atmospheric deposition across the mountainous terrain of Acadia National Park or Great Smoky Mountains National Park can be described by a GIS model that links empirical measurements to landscape features that are described in the GIS (Figure 1.6). Such spatially explicit models greatly enhance our ability to identify places on the landscape and times that may be subject to particularly high levels of atmospheric deposition (Weathers et al. 2006). GIS and other technologies are being used creatively and hold tremendous potential for understanding ecosystem processes across heterogeneous landscapes.

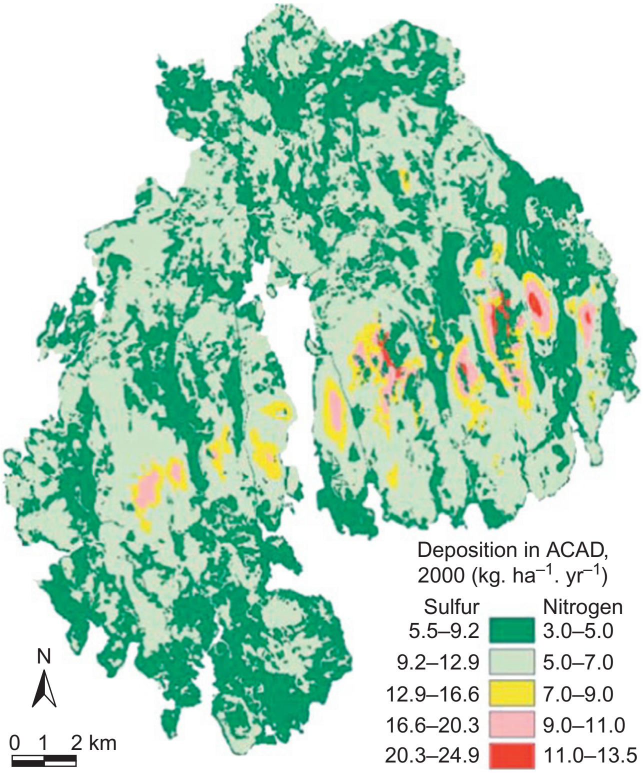

FIGURE 1.6 Atmospheric deposition of nitrogen and sulfur for the year 2000 to Mount Desert Island study area of Acadia National Park, Maine (ACAD). Deposition estimates are based on a GIS-based empirical model. *(From Weathers et al. 2006.)*

From There to Here: A Short History of the Ecosystem Concept in Theory and Practice

Ecosystem science is a relatively young discipline, largely developed since the mid-20th century (Hagen 1992; Golley 1993); the term "ecology" was coined only in 1866 by Ernst Haeckel. The concept of an ecosystem was first formally proposed by the English botanist Arthur Tansley in 1935, although related ideas were in circulation for at least a century before this. For instance, the idea of a biosphere (a region near the Earth's surface in which living organisms are a dominant geochemical force) was outlined by the French scientist Jean-Baptiste Lamarck in 1802; the term "biosphere" was coined in 1875 by an Austrian geologist, Eduard Suess, in describing the genesis of the Alps; and the concept of a biosphere was fully elaborated by the Russian mineralogist Vladimir Vernadsky in 1926. Other important precursors to the modern idea of the ecosystem included Karl Möbius' (1877) use of the term "biocoenosis" to refer to the biotic community associated with oyster beds;

Stephen Forbes' (1887) essay on "The Lake as a Microcosm," which explored the myriad of ecological interactions that existed within a bounded area (a lake) to produce a single system; and K. Friedericks' (1930) use of the idea of holocoens (Jax 1998). Although Vernadsky's ideas perhaps were closest to modern ideas of the ecosystem, they were not widely influential outside of the former USSR, and none of the other early concepts really captured the idea that organisms and their abiotic environment could be integrated into a single system.

In 1935, Tansley brought all of these ideas together by writing, "The fundamental concept appropriate to the biome [i.e., all living organisms] considered together with all the effective inorganic factors of its environment is the *ecosystem*." He further stated: "It is the systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth." Tansley's definition finally explicitly recognized the close interactivity (indeed the inseparability) of living and nonliving entities sharing the same physical space, and is remarkably similar to the definition of ecosystem that many ecologists use 80 years later. In 1942, just a few years after Tansley's paper appeared, Raymond Lindeman, a young American ecologist, published a paper laying out a conceptual framework that defined trophic levels and allowed the analysis of energy flow through ecosystems. Because modern ideas about element cycles had been around since the mid-19th century (Gorham 1991), much of the essential conceptual foundation for ecosystem science and its two major branches, element cycling and energy flow, was thus in place by 1942. However, it would take a few more decades before ecosystem studies formed a large part of ecology.

What remained was for the concept of ecosystems to be publicized and widely accepted by ecologists, and for scientists to find suitable tools for studying these newly defined "ecosystems." Of course, many scientists and techniques made important contributions to advance and shape what is now ecosystem science, but a few key contributions are worth special mention. Readers who are interested in more information about the development of the ecosystem concept and its use may want to read the detailed histories published by Hagen (1992), Golley (1993), and Kingsland (2005).

A key advance in the adoption of the ecosystem concept and approach by working ecologists was the appearance of Eugene Odum's popular textbook (1953, and especially 1959). Odum's textbook was organized around the ecosystem concept, and was enormously influential in introducing ecosystem science to generations of ecologists. This text showed with enthusiasm and clarity the possibility and value of quantitative, large-scale studies, how the ecosystem approach could be applied equally and simultaneously to both aquatic and terrestrial habitats, and the application of this approach for understanding complicated interactions and linkages at large scales (Likens 1992, 2001). Odum and his brother Howard T. Odum also conducted pioneering field studies showing how the ecosystem concept could be insightfully applied in nature (e.g., Odum and Odum 1955; Odum 1957). Odum's textbook was closely followed by a high-profile article in *Science* by Francis Evans (1956), which recommended the ecosystem as "the basic unit in ecology."

The first Big Science initiative in ecology, the International Biological Program (IBP) of 1964–1974, was organized around systems ecology and exposed hundreds of ecologists around the world to measurements of productivity, nutrient cycling, and decomposition, and the development of ecosystem models, despite controversy and criticism about the program (Committee to Evaluate the IBP 1975; Mitchell et al. 1976; Aronova et al. 2010). Thus, by the late 1960s, the basic ideas of ecosystem science were familiar to most ecologists.

Among all the tools that were developed with the science, we highlight two important advances here. First, radioisotopes were widely used in the 1940s through 1960s to trace movement of materials within and between ecosystems (see the earlier section "Tracers"). In the wake of the development of atomic weapons, agencies such as the United States Atomic Energy Commission (AEC) and equivalent agencies in other countries were looking for peaceful uses of radioactive materials. The timing of their interest and ability to provide funding coincided with the rise of ecosystem science, and led the AEC and similar agencies to provide radioisotopes and funding for many of the early studies on the movement of materials through ecosystems (Golley 1993).

Second, and more significantly, ecosystem scientists began to conduct large-scale experiments on entire ecosystems. As the essentially reductionist or bottom-up approach of the IBP showed, it is very difficult to understand or predict the behavior of entire complex ecosystems by measuring all of their many pieces and trying to model how the whole system will behave. Instead, a direct experimental approach can be used to cut through the Gordian knot of ecosystem complexity, and reliably show how the system actually reacts to some perturbation. It took a few decades for such whole-ecosystem experiments to become a common and accepted tool. Perhaps because of the pervasive influence of "The Lake as a Microcosm" and the clear boundaries to lakes, many of the earliest whole-ecosystem experiments were performed on lakes (Likens 1985; Carpenter et al. 1995). For instance, models and small-scale experiments were unable to resolve a bitter controversy in the 1960s about whether excessive phosphorus caused lakes to become offensively eutrophic; a whole-lake experiment was important (see Chapter 9). Likewise, by adapting the small-watershed technique from hydrology in the 1960s, ecosystem scientists could quantify inputs and outputs of materials to and from terrestrial ecosystems and treat entire watersheds as experimental subjects (Bormann and Likens 1967; Likens et al. 1970). Perhaps more than any other tool, whole-ecosystem experiments made Tansley's concept a practical subject of scientific study. Ecosystem experiments are now an important tool for scientists to study subjects as varied as the effects of toxicants, food-web structures, disturbances, and limiting nutrients in all types of ecosystems (Table 1.2).

As a result of these advances, during the period from approximately 1935 to 1975, ecosystem science moved from being just an interesting concept to a central position in contemporary ecology (Box 1.5). Ecosystem scientists, from the roots of the discipline to the present, have worked to unravel the complexity of entire ecosystems of all sizes and forms, from a water-filled cavity in a tree, to a small vernal pool, to a large lake, to a forested watershed, to an entire city, to the total biosphere. The ecosystem concept provides a comprehensive framework for study of the interactions among individuals, populations, and communities and their abiotic environments, and for study of the change in these relationships both temporally and spatially (adapted from Likens 1992).

BOX 1.5

Application of the Ecosystem Concept and Diversity among Ecosystem Scientists

You may have noticed the absence of women and people of color in the brief account of the early history and development of ecosystem science, which is in contrast to their frequent appearance elsewhere in the book. Although some women made important contributions to the practice of ecosystem science and allied fields (examples are given below), its early history was dominated by European and North American men. In fact, such dominance by European and North American men was a common feature of STEM (science, technology, engineering, and mathematics) fields and leadership in professional societies in the early to mid-20th century. For instance, between 1916 and 1980, only one of the 65 presidents of the Ecological Society of America was a woman (E. Lucy Braun), whereas during 2001–2020, nine of 20 presidents were women. Likewise, ecosystem science has diversified since the mid-20th century to include many more scientists from regions outside of Europe and North America. However, some geographic regions and groups of people still are badly underrepresented in the ranks of ecosystem science and other STEM fields. Diversifying our field is of utmost importance to advancing the science (e.g., Nielsen et al. 2017); it remains an important challenge for ecosystem science to meet.

E. Lucy Braun documented the immense diversity of forest types within the temperate broadleaf forest biome, and highlighted the deep history of change since glacial times. Insights about ecosystem heterogeneity and history are important parts of contemporary ecosystem ecology, fueled in part by Braun's work. She was also the first female president of the Ecological Society of America (ESA) in 1950. (Source: https://www.wvxu.org/post/wcet-tv-premieres-force-nature-lucy-braun-oct-7#stream/0https://images.app.goo.gl/hc6uKekPGR6AypWj9.)

Through her groundbreaking work in identifying the prevalence and concentration of pesticides, specifically DDT, in ecosystems, Rachel Carson's work exemplifies the application of ecosystem science to toxicology as well as policy and conservation advocacy, and underpinned the formation of both the National Resource Defense Council (NRDC) and the Environmental Protection Agency (EPA) (see www.nrdc.org/stories/story-silent-spring). (Source: Rachel Carson examining a specimen, Alfred Eisenstaedt/The LIFE Picture Collection/Getty Images from https://www.nrdc.org/stories/story-silent-spring.)

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