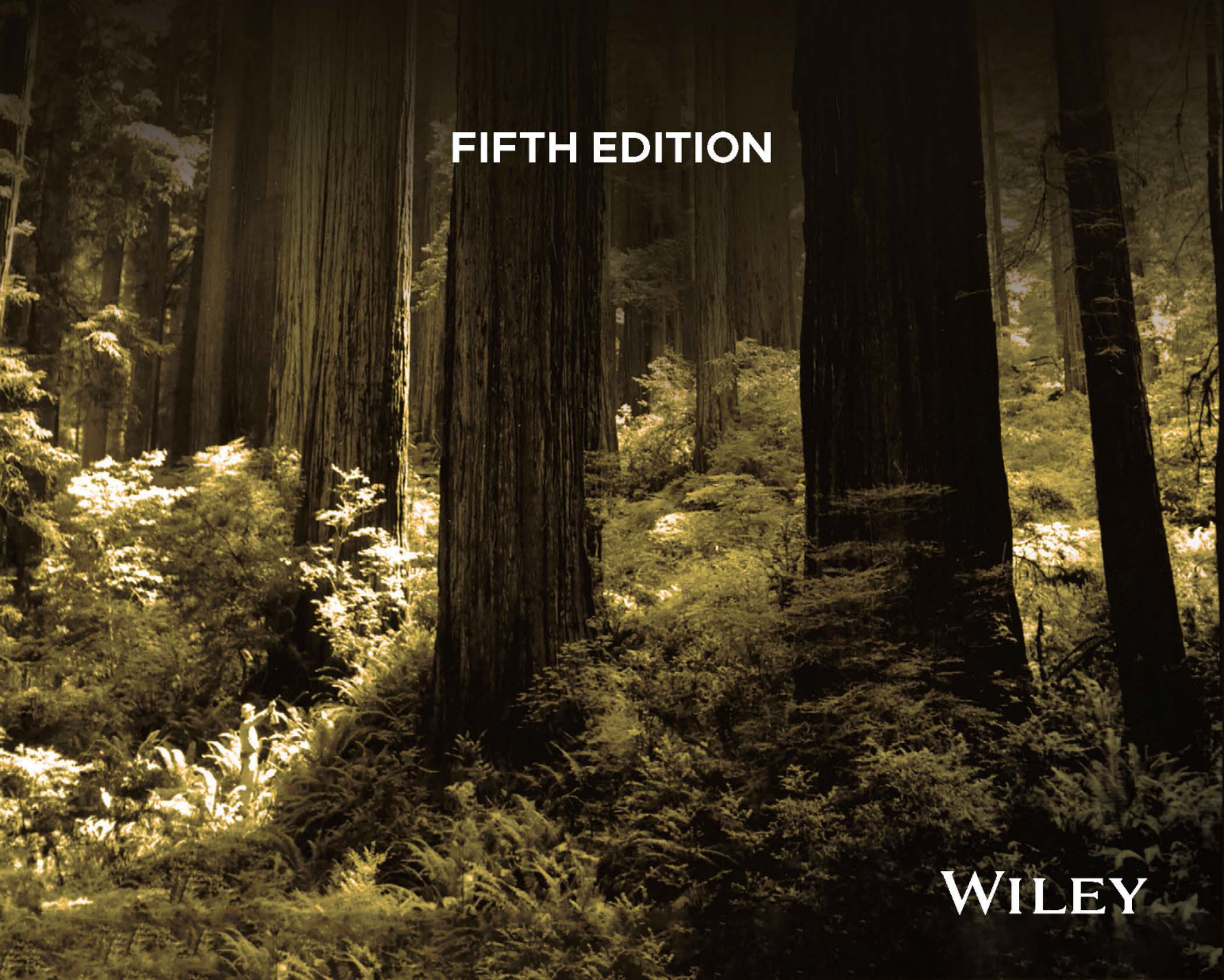
FOREST ECOLOGY

DANIEL M. KASHIAN • DONALD R. ZAK
BURTON V. BARNES • STEPHEN H. SPURR



FIFTH EDITION

WILEY

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Dedication

We dedicate the 5th edition of Forest Ecology to the co-author of the 2nd and 3rd editions and the lead author of the 4th edition, *Burton V. Barnes* (1930–2014). It would be no easy task to find a more accomplished and humble leader in his field. He excelled at his science, was a truly beloved teacher, and helped to shape the world view of thousands of colleagues, friends, students, managers, and scientists alike, all with an unmatched humor and a love of the natural world.

Burt Barnes was world-renowned as an expert in the ecology of North American aspens and the ecological classification of forest ecosystems. His professional training was in forest ecology, botany, and genetics, but he dabbled heavily in glacial geomorphology, soil science, phytogeography, and woody plant physiology. Perhaps his greatest love, however, was teaching, especially in the field, which drove his motivation for this textbook. Generations of students have been touched by his love for the art and science of teaching field ecology, which they will forever pass on to future generations. We, as authors of this edition, have been personally and professionally shaped by him as a mentor, colleague, and friend. His legacy is therefore unending. To him we say, in his own words, "Thanks for everything you have done—and will do."

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Preface

Forest Ecology deals with forest ecosystems—spatial and volumetric segments of the Earth—and their climate, landforms, soils, and biota. It is designed as a textbook for people interested in forest ecosystems—either in the context of courses in forest ecology and environmental science or as an ecological reference for those in professional practice. This book is meant to provide basic ecological concepts and principles for field ecologists, foresters, naturalists, botanists, and others interested in the conservation and restoration of forest ecosystems.

Ecology, in general, has undergone several sea changes since the appearance of the first edition in 1964, with enormous increases in public interest and scientific development of theory and research. Ecology and the issues associated with it have become part of our modern lexicon. The great number of advances in our ecological knowledge, as well as increased public interest, presents forest ecologists with both opportunities and challenges to sustainably manage ecosystems using our best understanding of ecosystem properties and processes. This book will hopefully be useful in that process by providing an understanding of the ecological relationships of individual trees and forest ecosystems.

The book has six major subdivisions. "Forest Ecology and Landscape Ecosystems" introduces forests as whole ecosystems rather than tree communities, and at multiple scales. "The Forest Tree" considers the genetic variations among individual trees, the causes of diversity within and between species, regeneration ecology, and selected aspects of tree structure and function. "The Physical Environment" treats the physical factors of forest ecosystems that form the forest site—the influences of light, temperature, physiography, soil, and fire on the individual forest plant and on plant communities. The concluding chapter in this part considers methods of evaluation and classification of the forest site and ecosystems. In Part 4, "Forest Communities," we consider the forest community of trees and associated plants and animals that form a key structural component of forest ecosystems—one part of the whole. We also consider the importance and measurement of diversity of species and ecosystems. In "Forest Ecosystem Dynamics," we examine the functional relationships of the physical environment and the biota. We first examine changes in communities and ecosystems over tens of thousands of years. We then consider the extent to which disturbance, an ecosystem process, initiates change (termed succession) over shorter time scales of centuries. Chapters on carbon balance and nutrient cycling present a detailed consideration of the pattern in which carbon (i.e., energy) and plant nutrients flow within forest ecosystems and how natural and human-induced disturbances alter these patterns. Finally, "Forests of the Future" explores the role of humans in the sustainability of forests. Here we emphasize two of the most pressing issues in forest ecology today, climate change and invasive species, and present a review of landscape ecology which has humans at its center. We end the book with a treatment of sustainability itself.

In this edition, we have made great attempts to maintain the core organization and readability of previous editions while adding those areas most relevant to forest ecology that have developed over the last quarter-century. We have retained the important focus on landscape ecosystems (rather than organisms and communities) that was developed in the fourth edition and have added critical new ecological concepts and research that have developed in genetics, diversity, climate change, invasive species, and sustainability. The ecological literature has only become more voluminous over the past 25 years, and as in previous editions our use of the literature was selective, rather than exhaustive. New references were most often chosen based on their accessibility to students and practitioners as understandable examples of important ecological concepts. At the same time, we have retained many older references that still provide excellent examples of fundamental ecological concepts, many of which would otherwise be lost in obscurity.

As before, we have integrated woody plant physiology into multiple chapters, rather than developing it in a single chapter, and in this edition have done the same with climate because of its overriding influence on so many ecosystem processes. We have also further limited our treatment of forest ecology with examples from temperate and boreal forests, with special emphasis on North America and Europe. With a primary focus on the ecological principles of forests that form the basis for management, we have largely avoided specific treatments of forest management techniques and strategies throughout the book, although by necessity we have provided some examples of forest management in the chapters on diversity and invasive species.

The revised edition would not have come to pass without the patience and dedication of many colleagues who helped in its preparation. We are especially indebted to the following for their reviews of one or more chapters: Dennis Albert, Brian Buma, Mark Dixon, Tom Dowling, Jennifer Fraterrigo, Stephen Handler, Donna Kashian, Doug Pearsall, David Rothstein, Madelyn Tucker, and Chris Webster. Other important contributions, either through provision of material, enlightening discussions, or enthusiastic encouragement, were made by Jonathon Adams, Virginia Laetz, and Dan Binkley. Victoria Meller was extremely supportive of D. M. Kashian and his time spent away from campus in the completion of this revision, as were the graduate students in the Kashian lab. Perhaps without knowing it, the graduate and undergraduate students in the 2018 and 2020 Terrestrial Ecology classes at Wayne State had an immense role in the thought processes and revisions made in the 5th edition. D. R. Zak was partially supported by the National Science Foundation and the Department of Energy during the preparation of this text.

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Forest Ecology and Landscape Ecosystems

PART 1

Forest ecologists work to understand the dynamics, structure, and function of forest ecosystems. The first step in doing so is to approach ecosystems as geographic units or landscape ecosystems—real, three-dimensional, defined locations at the Earth's surface. Landscape ecosystems include organisms, species, and communities, but also the air above and the soil below these living things such that organisms are but one important part of a larger landscape unit. Our perception of forest ecosystems in this book is that ecosystems are not simply extensions of forest communities, whereby ecosystems are conceived as organisms and their environment. Instead, units of whole ecosystems that integrate factors of climate, landforms, soils, co-occurring biota, and all the interactions between them are the most appropriate units of study rather than their individual parts that too often claim our immediate attention.

In understanding forest ecosystems, particularly in the context of an ecology course or in solving ecological problems, ecosystems need to be conceived at several spatial and temporal scales. It is very daunting to attempt to gain such understanding, and certain well-known ecologists have suggested that the environmental complex is unknowable and inexpressible. However, conceiving landscapes as ecosystems and proceeding "from above," that is, from the biggest to the smallest units to understand their spatial relationships, makes synthesis possible and manageable. Although local sites and stands with their familiar species appear a convenient starting point, we know that these are, in turn, affected by geological and climatic factors of higher levels within which they are embedded. Landscape ecosystems are nested within one another in a hierarchy of spatial sizes such that it is best to consider the big picture first—the comprehensive view from the outside—rather than the minutia of details as seen from inside of the ecosystem. Our perspective in understanding ecosystems involves establishing a framework for studying the components—a framework of the spatial and temporal, hierarchical pattern of ecosystems of all sizes making up the ecosphere.

Therefore, in the first part of this book, before immersing in the detail of organisms, sites, and their interrelationships, we wish to first examine landscape ecosystems, and then place them within a perspective of spatial levels and their processes at different

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temporal scales. In Chapter 1, we present the basic concepts of forest ecology within a framework of landscape ecosystems. In Chapter 2, we present the concept of scale and consider the hierarchy of these landscape ecosystems. These fundamental concepts provide the basis for studying the variation, life history, and ecology of individual organisms that follow in Part 2.

Concepts of Forest Ecology

CHAPTER 1

A **forest** is an ecological system dominated by trees and other woody vegetation. More than simply a stand of trees or a community of woody and herbaceous plants, a forest is a complex ecological system, or **ecosystem**, characterized by a layered structure of functional parts. **Ecology** is the study of ecological systems and their interacting abiotic and biotic components. **Forest ecology**, therefore, addresses the structure, composition, and function of forests. In forest ecology, we study forest organisms and their responses to physical factors of the environment across forested landscapes. Forests are widespread on land surfaces in humid climates outside of the polar regions. It is with forests in general, and with the temperate North American forest in particular, that this book is concerned.

There are many ways to study forest ecosystems. Most simply, a forest may be considered in terms of the trees that give the forest its characteristic aboveground appearance or **physiognomy**. Thus, we think of a beech–sugar maple forest, a ponderosa pine forest, or of other **forest types**, for which the naming of the predominant trees alone serves to characterize the forest ecosystem. Forest types are often considered to be composed of **forest stands**, which are trees in a local setting possessing sufficient uniformity of species composition, age, spatial arrangement, or condition to be distinguishable from adjacent stands (Ford-Robertson 1983).

A broader concept of a forest may take into account the interrelationships that exist between forest trees and other organisms. Certain herbs and shrubs are commonly found in beech–sugar maple forests, and these may differ from those found in ponderosa pine or loblolly pine forests. Similar interrelationships may be demonstrated, for example, for birds, mammals, arthropods, mosses, fungi, and bacteria. Thus, part of the forest ecosystem is the assemblage of plants and animals living together in a **biotic community**. The **forest community**, then, is an aggregation of plants and animals living together and occupying a common area. It is thus a more organismally complex unit than the forest type.

A third approach is to focus on geographic or **landscape ecosystems**. This approach is centered conceptually and in practice on whole ecosystems and not just their parts. When our primary focus is real live chunks of Earth space, that is, landscapes and waterscapes (oceans, lakes, rivers; hereafter included as parts of a landscape), we can effectively study their parts (e.g., organisms, soils, and landforms) while recognizing that each is but one part of a functioning whole. We emphasize this focus on ecosystems rather than on the individual organisms and species that are parts of them.

In the past, the forest stand or the species has been the focus in natural resource fields such as forestry and wildlife. However, we are really managing whole forest ecosystems, despite their incredible complexity, because the diverse biota is inseparable from the physical environment that supports it. A consideration of the field of ecology from this viewpoint provides an overall perspective.

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ECOLOGY

Broader fields of scientific inquiry are difficult to limit and define, and ecology is one of the most indistinct. In 1866, Ernst Haeckel proposed the term **oecology**, from the Greek *oikos* meaning home or place to live, as the fourth field of biology dealing with environmental relationships of organisms. Thus, ecology literally means “the knowledge of home,” or “home wisdom.” Since its introduction, the term has been applied at one time or another to almost every aspect of scientific investigation involving the relationship of organisms to one another or to the environment (Rowe 1989). Haeckel’s organismal focus of ecology has since been redefined and expanded to include the physical aspects of the environment that provide life for those organisms (Hagen 1992; Golley 1993). Thus, Rowe (1989, p. 230) suggests:

> *Ecology is, or should be, the study of ecological systems that are home to organisms at the surface of the earth. From this larger-than-life perspective, ecology’s concerns are with volumes of earth space, each consisting of an atmospheric layer lying on an earth/water layer with organisms sandwiched at the solar-energized interfaces. These three-dimensional air/organisms/earth systems are real ecosystems—the true subjects of ecology.*

This approach to ecology emphasizes whole ecosystems as well as organisms, both volumetric and having structure and function.

LANDSCAPE ECOSYSTEMS

The British botanist–ecologist Arthur Tansley (1935) introduced the term ecosystem, writing with an emphasis on “the whole ‘system,’ including not only the organism complex but also the whole complex of physical factors.” He also noted that from the point of view of the ecologist, ecosystems “are the basic units of nature on the face of the Earth.” Tansley was a biologist and vegetation ecologist, and so his idea of ecosystem was centered on organisms (species or communities) rather than geographic or landscape entities. With this **bioecosystem** approach, “ecosystem” derives its meaning from particular plant or animal organisms of interest, and an “abiotic” environment defined by the organisms as relevant or not is considered with lesser emphasis. In this approach, every organism defines its own ecosystem, nearly infinite in number and difficult to study and use as a basis for management and conservation.

On the other hand, others (e.g., Rowe 1961a and Troll 1968, 1971) view ecosystems centered on geographic or landscape units (i.e., **geoecosystems)** of which organisms are but one important structural component (Rowe and Barnes 1994). We term these units **landscape ecosystems** in part to differentiate them from geology-based units of study (e.g., Huggett 1995). Landscape ecosystems are geographic objects, with a defined place on the Earth. Landscape ecosystems have three dimensions (volume) just as organisms do, including landforms and biota at the Earth’s surface as well as the air above them and the soils below them (Figure 1.1). Other terms have been introduced to express the same idea, but are less commonly used, such as the ecotope (Troll 1963a, 1968) and the ecoterresa (Jenny 1980). This geographic/volumetric concept has been discussed and adapted by professional and academic ecological societies (Christensen et al. 1996), and is useful to field ecologists, naturalists, foresters and other land managers, and natural resource professionals. The concept is described in detail in Chapters 2 and 11.

In addition to being geographic and volumetric, landscape ecosystems are hierarchical, extending downward from the largest ecosystem we know, the **ecosphere** (Cole 1958), through multiple levels of ecological organization (Figure 1.2). These levels include macrolevel units of continents and seas, each of which contains mesolevel units of regional ecosystems (major physiographic units and their included organisms), which in turn contain local ecosystems (Hills 1952), the smallest level of homogeneous environment with organisms enveloped in it. We therefore conceive the ecosphere and its landscapes as ecosystems, large and small, nested

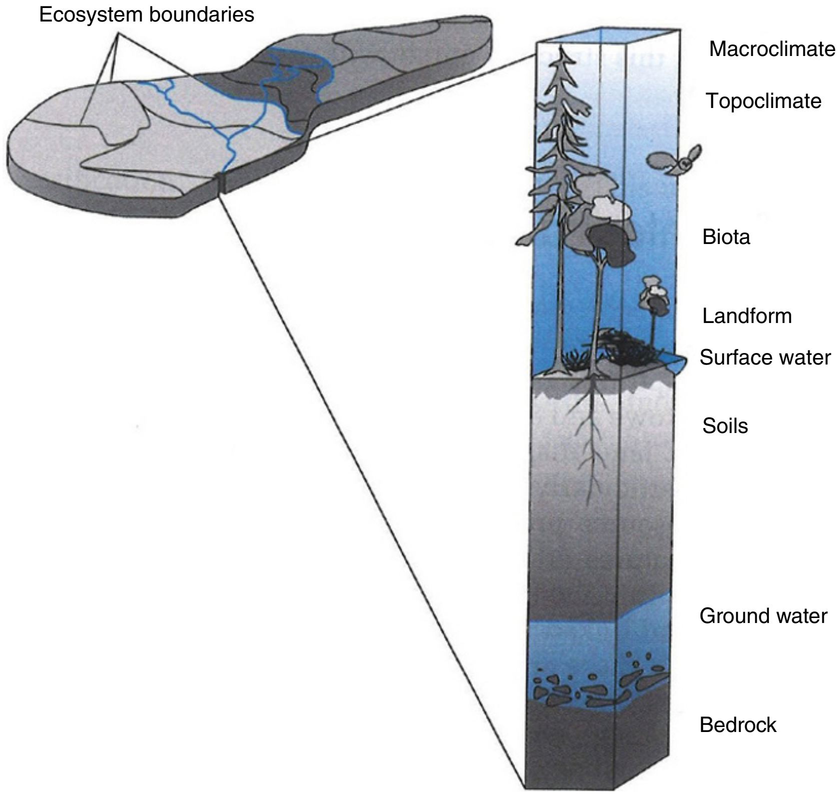

FIGURE 1.1 The three-dimensional, volumetric nature of a landscape ecosystem. Ecosystems comprise the atmosphere (macroclimate as well as the climate affected by surface relief), landforms and soils (underlain by ground water and bedrock), and the biota that provide a physical connection between the air and the Earth. *Source:* Bailey (2009) / Springer Nature.

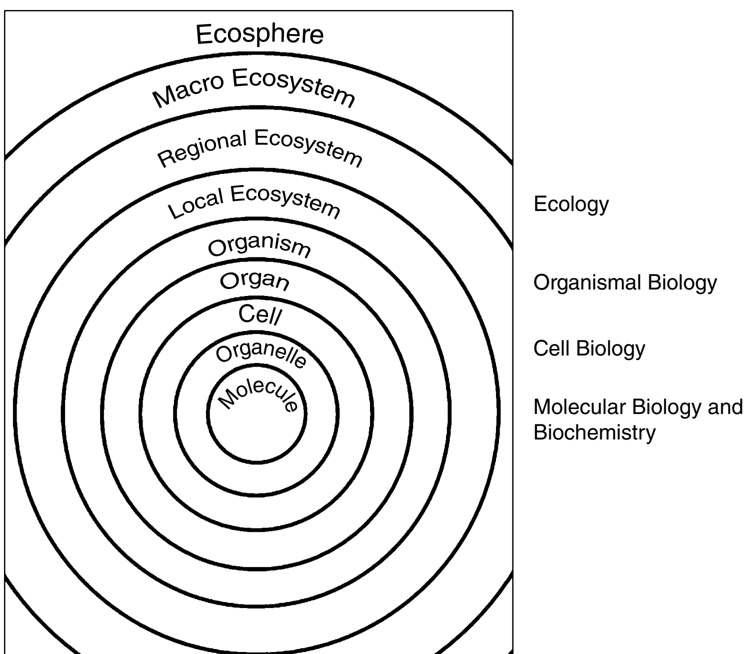

FIGURE 1.2 Objects of study from the most inclusive (ecosphere) to the least inclusive levels of organization (cell and organelle and molecule below it). Note that each higher level envelops the lower ones as parts of its whole. Some corresponding fields of study are also shown. Aggregates of organisms, such as populations and communities, are components of ecosystems at all scales. Like other components such as atmosphere, landform, and soil, they do not appear in this diagram of first-order objects of study, but are shown in Figures 1.3 and 1.4. *Source:* Modified from Rowe (1961a).

within one another in an ecological hierarchy, having processes at each level with their own spatial and temporal scales (see Chapter 2).

Two landscape ecosystems in Figure 1.3 (Rowe 1984b) illustrate characteristic ecosystem differences in hilly or mountainous terrain. The two ecosystems are distinguished by different geomorphologies (convex upper slope versus concave lower slope, and high versus low topographic slope position) that mediate microclimate, soil water, and nutrient availability. The vertical dashed line is placed at an ecologically significant boundary that spatially separates the two ecosystems. Organisms in these ecosystems are sandwiched between the air and the Earth. Also shown in Figure 1.3 are the traditional fields of study in which individuals seek to understand each of the ecosystem components, although forest ecologists aim to understand the integrated effects of all of these components.

In many parts of this book, we focus on organisms, species, and communities, but always remembering that they are parts of volumetric, hierarchical ecosystems. For studies of organisms in their immediate surroundings, a biological approach is often useful. Nevertheless, for management of ecosystems, studies of forest productivity, and the conservation and restoration of forest ecosystems, a landscape ecosystem approach is eminently practical and theoretically sound. Forest ecologists not only study (i) organisms of these systems and their aggregates as communities

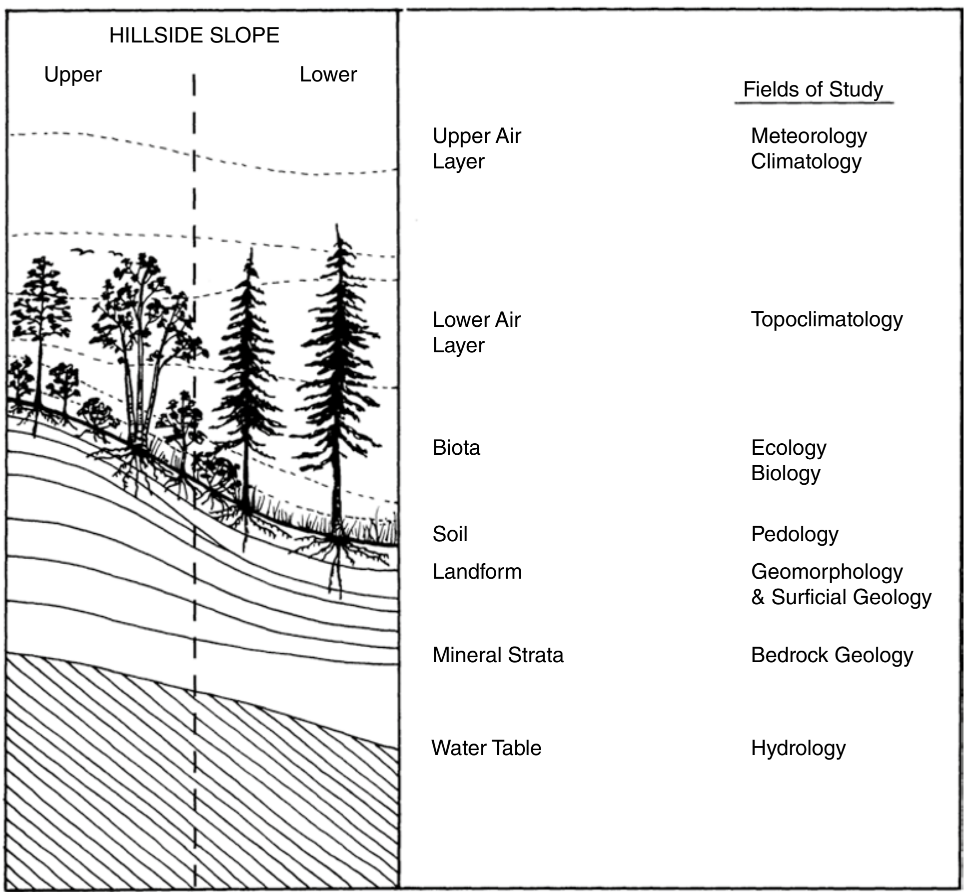

FIGURE 1.3 Structural profile illustrating landscape ecosystems of upper and lower slopes. Air–earth layers surround the organisms at the Earth's energized surface. The vertical line is set at an ecologically significant topographic break, dividing the upper and lower slope ecosystems. *Source:* Rowe (1984b) / United States Department of Agriculture / Public Domain.

and populations (see Chapters 3–5, 12, and 13), but also (ii) the functioning of local ecosystems that involves complex interactions among organisms and their supporting environment (Chapters 6–11, 13–14, and 16–19), and (iii) the spatial patterns of occurrence and interrelationships of entire forest ecosystems (Chapters 2, 18, 19, and 22).

LANDSCAPE ECOSYSTEM AND COMMUNITY

The term ecosystem was introduced in 1935 by Tansley, but terms in various languages, such as taiga, heath, bald, Auenwald (river floodplain forest), pampas, prairie, chaparral, maquis, hammock, muskeg, and bog, have long been used to depict interactions among air, organisms, and soil. Very often the terms emphasize a distinctive plant community and may therefore imply that an ecosystem is simply an extension of a community. Tansley's definition of ecosystem as "organism + environment" leads to this view, and general definitions such as "ecosystem = biotic community + environment" reinforce this view. Although indispensable for forest ecologists and managers, vegetation may not always coincide with climate–landform–soil-based ecosystems because of disturbance and/or unknown historical factors. Thus, we emphasize the importance of geography and physiography within a regional climatic setting as the basis of understanding not only vegetation but whole ecosystem structure and function.

This conceptual approach is not to say that communities are unimportant; they form the key ecosystem component whose response is essential in affecting ecosystem change and indicating the integrated effects of many site factors (Chapter 11). Communities and populations, however, fundamentally differ from entities such as ecosystems, organisms, and cells because they are aggregates of individuals but *not functional systems*. Entities such as ecosystem, organism, cell, and molecule (Figure 1.2) are "volumetric" levels of organization because they have structurally joined parts that form a functioning unit (Rowe 1961a, 1992c). By contrast, communities and populations are assemblages or aggregates of spatially separated trees and understory plants that have no necessary, physical, structural connections.

ECOSYSTEM STRUCTURE AND FUNCTION

An ecosystem's structure describes the spatial arrangement of its parts. In local forest ecosystems, multiple strata of atmosphere and soil (Figure 1.3), as well as surface relief, influence species composition and its patterns of occurrence. Plants provide a physical connection between the soil strata and the aboveground layers of air. The layered structure and related physical and chemical properties of soil are well studied and understood, but similar properties of the atmosphere are not (Rowe 1961a; Woodward 1987), particularly as they affect forest organisms at the Earth's surface. Vegetation itself is also structured vertically, and the vertical structure and species composition of communities as well as species interactions provide insights critical in understanding properties and processes of ecosystems. In addition to species composition, vegetation structure is shaped by tree form and stem density, canopy characteristics, shrub and herbaceous plant abundance, and the amount and distribution of dead vegetation, among other characteristics. Thus, the physiognomy of vegetation varies markedly in different regional and local ecosystem types (Chapters 5 and 6).

The horizontal spatial patterning of these structural components occurs at multiple spatial scales, but is most often described across broad scales. Landscapes are structured horizontally into mosaics of ecosystems that reflect differences in climate, geology, and physiography and their relative effects on vegetation. The natural communities of these systems reflect limiting factors of climate, soil water, nutrients, and disturbances, and in turn modify the physical factors. Different ecosystem mosaics characterize mountains, plains, and river valleys due to fundamental differences in their physical factors and the vegetation adapted thereto (Chapter 8). The diversity of landscape ecosystems can be assessed by understanding such mosaics (Lapin and Barnes 1995). Such an understanding provides a spatial ecosystem framework for programs in biodiversity that seek to conserve and manage the diversity of organisms and maintain and increase populations of rare and endangered species (Chapters 14 and 22).

Local landscape ecosystems, besides having a structure of interconnected parts, are functional units characterized by many processes that define their properties. Ecosystem-level processes are part of the entire system and are not restricted only to physical or biotic parts. These processes drive or mediate the flow of energy or matter and/or the cycling of materials in the system. Organic matter decomposition; cycling of water, nutrients, and carbon; and biomass accumulation are considered ecosystem-level processes. Other processes are often more associated with plant species, populations, or communities, such as photosynthesis and respiration, reproduction, regeneration, mortality, and succession. Despite their basis in organisms, these are also ecosystem processes because they are mediated and regulated by characteristic ecosystem factors of temperature, water, nutrients, and disturbances (such as fire, windstorm, and flooding). Ecosystem function is often described with box-and-arrow diagrams, flow charts, and simulation modeling as ways of disentangling very complex systems (Figure 1.4).

Landscape ecosystem structure and function are tightly coupled by the physical environment, the frequency and severity of disturbances that reset succession, and the life histories of the plants and animals that comprise the biotic community. There is increasing evidence that many aspects of an ecosystem's function are linked to the diversity of its biota (Chapter 14). In turn, an

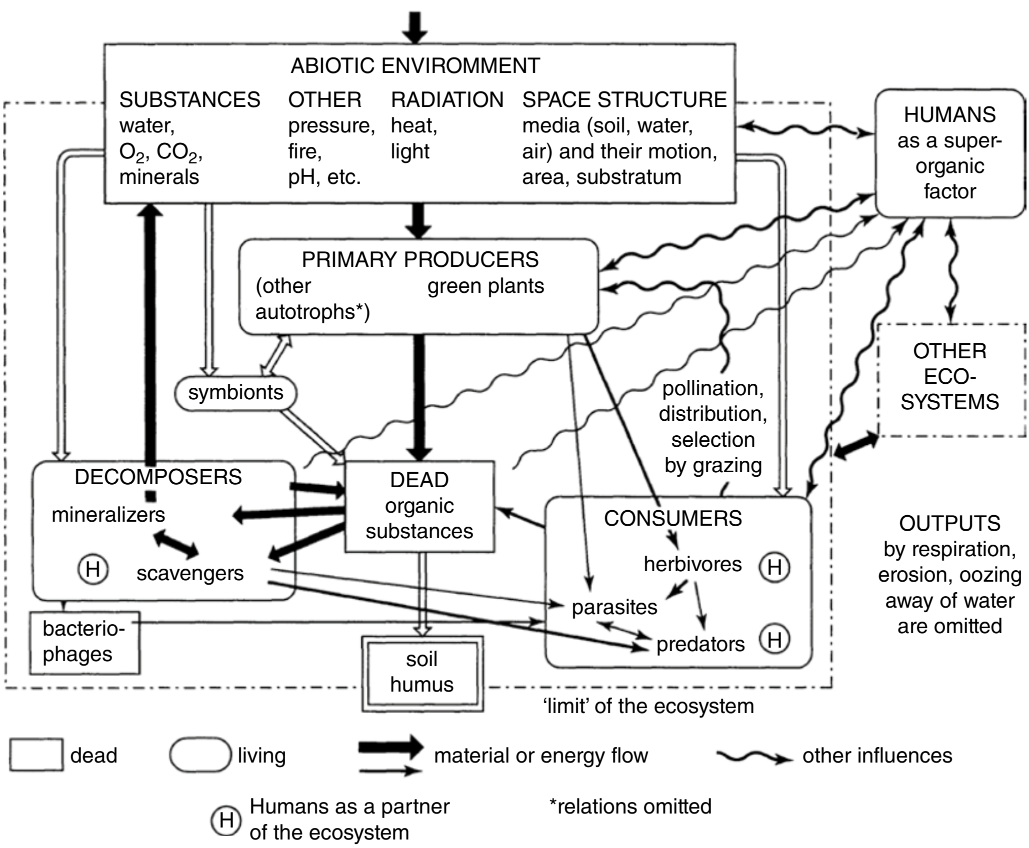

FIGURE 1.4 A model of a landscape ecosystem detailing the flow of energy and matter among biota. The model also describes the interactions between the physical environment and the biota. *Source:* Reprinted from Ellenberg (1988) / Cambridge University Press.

ecosystem's biodiversity is strongly shaped by its physical factors such as climate, physiography, and soil, which provide the context within which organisms survive, adapt, and evolve. In addition, the functional aspects of an ecosystem are strongly affected by its geographical context and by its spatial position relative to its surrounding neighbors on a landscape. Adjacent ecosystems, especially in mountainous or hilly terrain, affect one another by the lateral exchanges of materials and energy. Water and snow, soil, organic matter, nutrients, and seeds are transported downhill; the effects on other ecosystems depend on the size, shape, and composition of the systems. Therefore, an understanding of the spatial pattern and configuration of landscape ecosystems can play an important role in the management of ecosystems and their biota. An excellent overview of function in terrestrial ecosystems is given by Chapin et al. (2012), its variation across landscapes considered in Lovett et al. (2005), and the history of the ecosystem concept itself is reviewed by Golley (1993).

EXAMPLES OF LANDSCAPE ECOSYSTEMS

There are many examples of landscape ecosystems, some of which are easily discerned in the field, whereas others must be carved out of geographic continua. For example, bogs in the glaciated terrain of northern and boreal regions are easily discernible ecosystem types. They exhibit distinctive physiography, soil, and vegetation, and they recur in the landscape. The distinct terraces of river floodplains distinguish local ecosystem types that differ in microclimate, soil, drainage, vegetation, and their dynamics. Mountains are characterized by gradients of elevation, aspect, and slope steepness along which strikingly different ecosystems can be purposefully delimited and mapped, although their boundaries may not be sharply demarcated. On old lake-bed terrain, dry, sandy beach ridges are easily distinguished from adjacent depressions of swampy land. Differences in water drainage and oxygen availability in these adjacent systems result in major differences in their native tree- and ground-flora vegetation. Unseen but critical are the very different processes that also distinguish these ecosystems.

Ecosystem components will change over time, giving rise to a sequence of different landscape or waterscape ecosystems on a given place on the Earth's surface. Striking changes in the fossil record illustrate long-term changes in physiography, soil, and biota (Chapter 15), but short-term changes also occur. Shorter-term changes are most obvious when natural or human-caused disturbances affect vegetation. A site-specific location may exhibit a range of different forest communities over 100 to 300 years, young and old, as disturbances or lack thereof affect the biota. Ecosystem structure and function at this site change over time. The landforms and associated pattern of parent material, soil, and climate also change over time, but more slowly than the suite of species available to recolonize the disturbed site. Thus, what we term the **ecosystem site type** or simply **ecosystem type** (land area supporting potentially equivalent ecosystems) can be distinguished and mapped regardless of the forest community currently present.

One such example is illustrated in Figure 1.5 where deciduous forests occur on glaciated terrain in southern Michigan. In this setting, three local *ecosystem types* are distinguished by differences in physiography (outwash and moraine landforms); soil; drainage; and overstory, understory, and ground-cover vegetation. The relatively fine-textured, silty soil on the outwash plain (type 1) supports forest dominated by white oak, whereas the drier, coarse-textured, sandy outwash soil (type 2) supports a black oak community. The fine-textured, moist, clayey soil on the rolling moraine landform (type 3) supports a community dominated by northern red oak. The moraine formerly supported a beech–sugar maple forest. However, recurrent fires through the drier white and black oak ecosystems killed the fire-sensitive mesic species of the adjacent moraine ecosystem and led to dominance of northern red oak. An occasional beech is still found, and red maple has invaded the shaded understory.

The western portion of ecosystem type 1 was clear-cut about 90 years ago, and a *cover type* markedly different from the adjacent old-growth white oak forest has formed (Figure 1.5, type