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

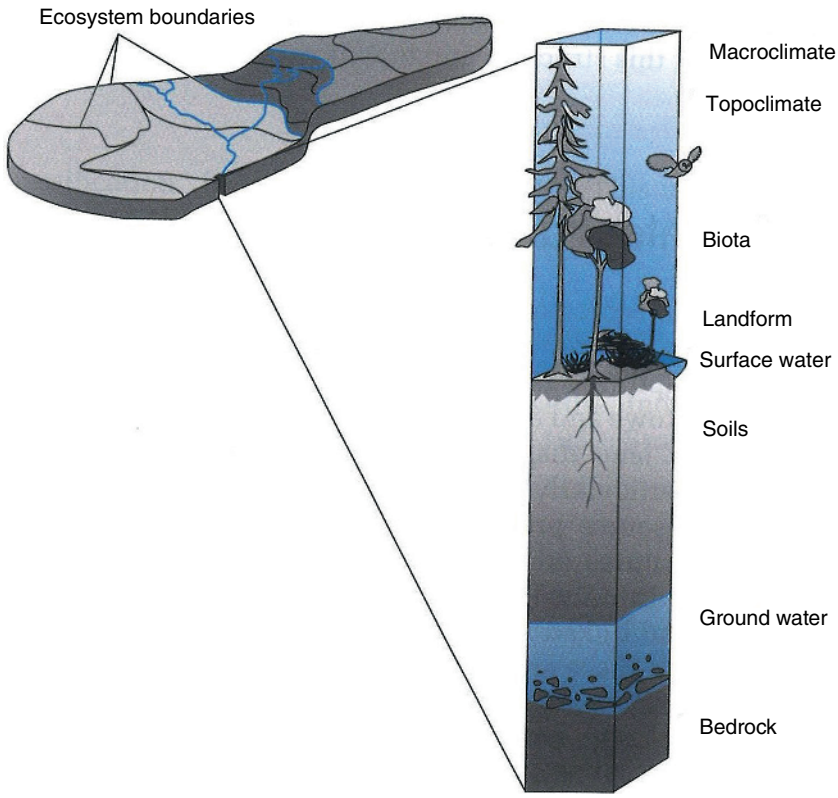

FIGURE 1.1 The three-dimensional, volumetric nature of a landscape ecosystem. Ecosystems comprise the atmosphere (macroclimate as well as the climate affected by surface relief), landforms and soils (underlain by ground water and bedrock), and the biota that provide a physical connection between the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

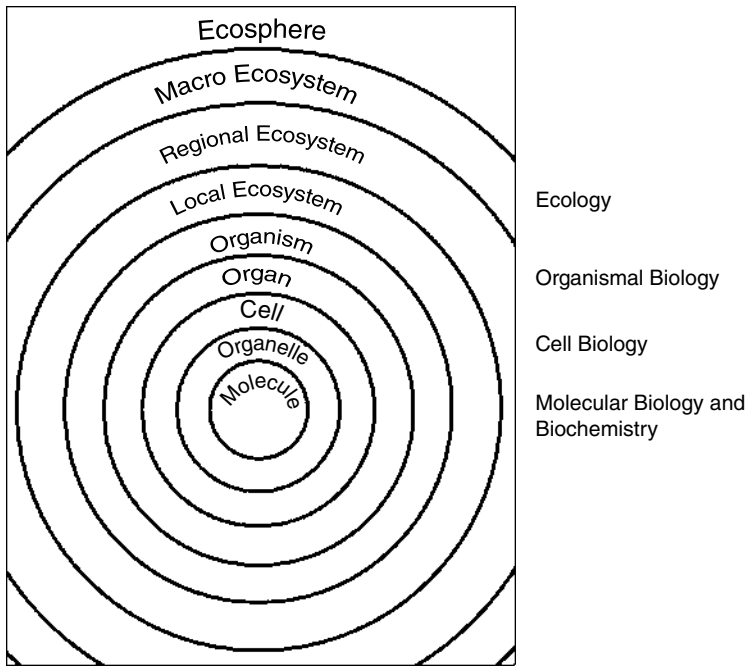

FIGURE 1.2 Objects of study from the most inclusive (ecosphere) to the least inclusive levels of organization (cell and organelle and molecule below it). Note that each higher level envelops the lower ones as parts of its whole. Some corresponding fields of study are also shown. Aggregates of organisms, 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

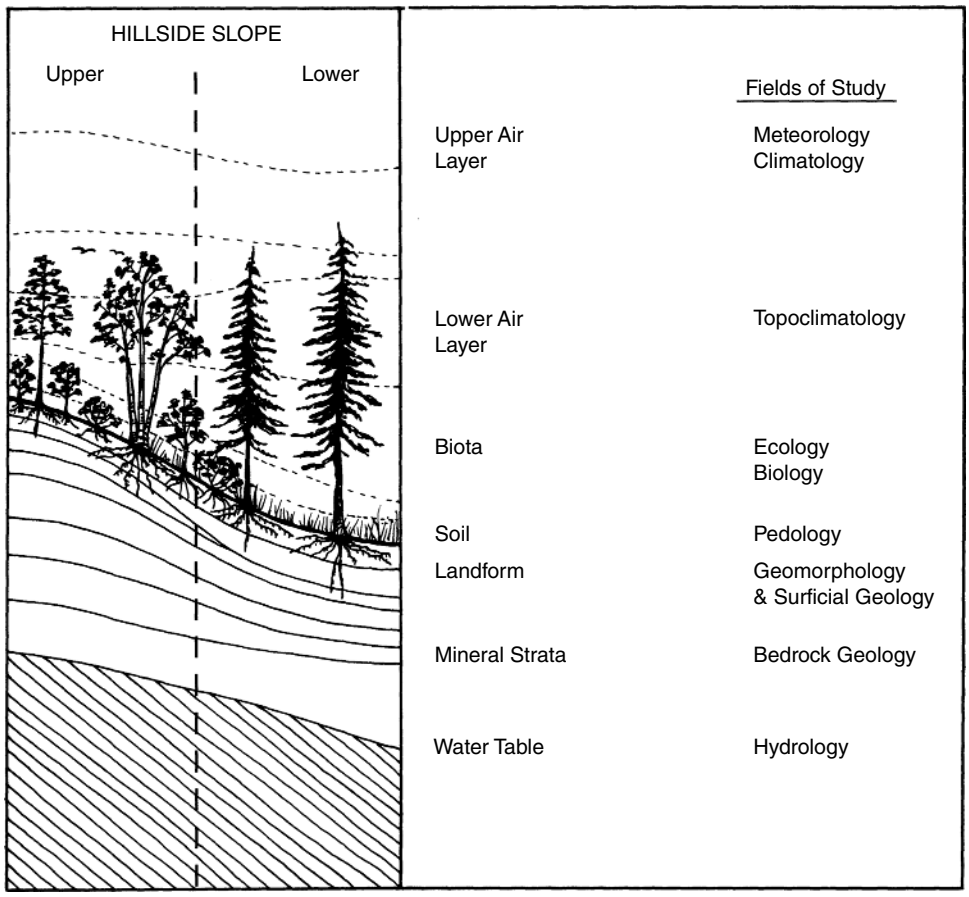

FIGURE 1.3 Structural profile illustrating landscape ecosystems of upper and lower slopes. Air–earth layers surround the organisms at the Earth's energized surface. The vertical line is set at an ecologically significant topographic break, dividing the upper and lower slope ecosystems. *Source:* Rowe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

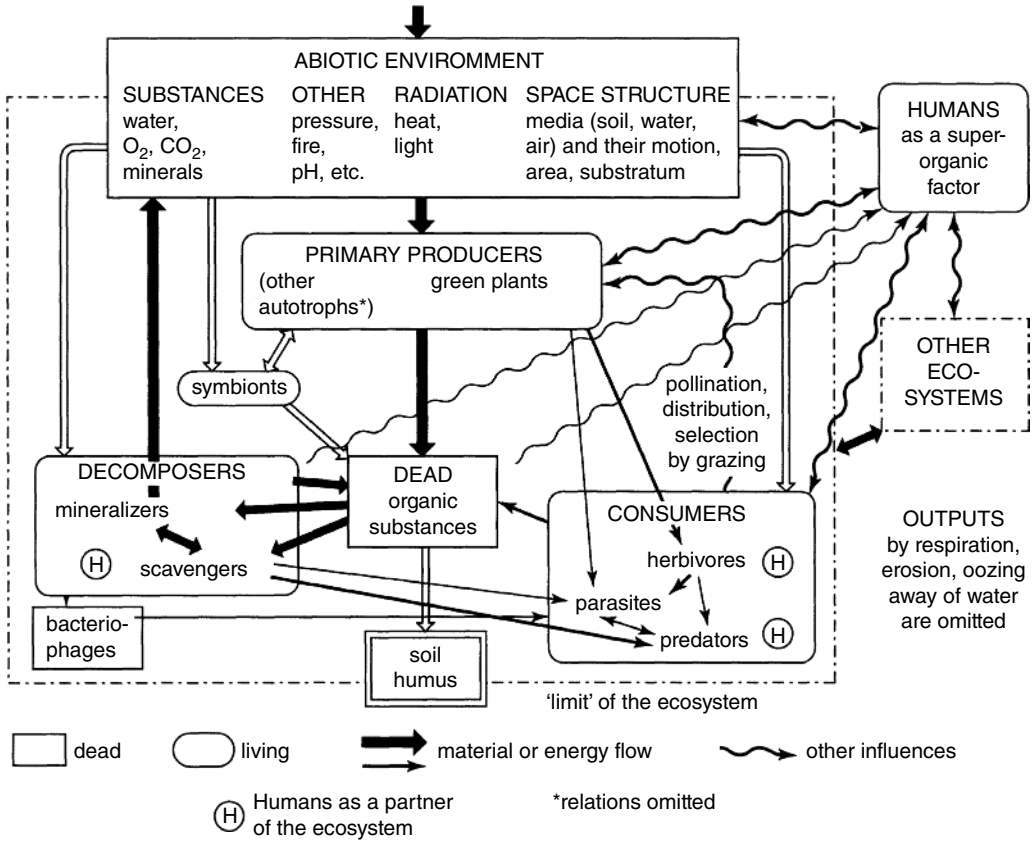

FIGURE 1.4 A model of a landscape ecosystem detailing the flow of energy and matter among biota. The model also describes the interactions between the physical environment and the biota. *Source:* Reprinted from Ellenberg (1988) / Cambridge University Press.

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

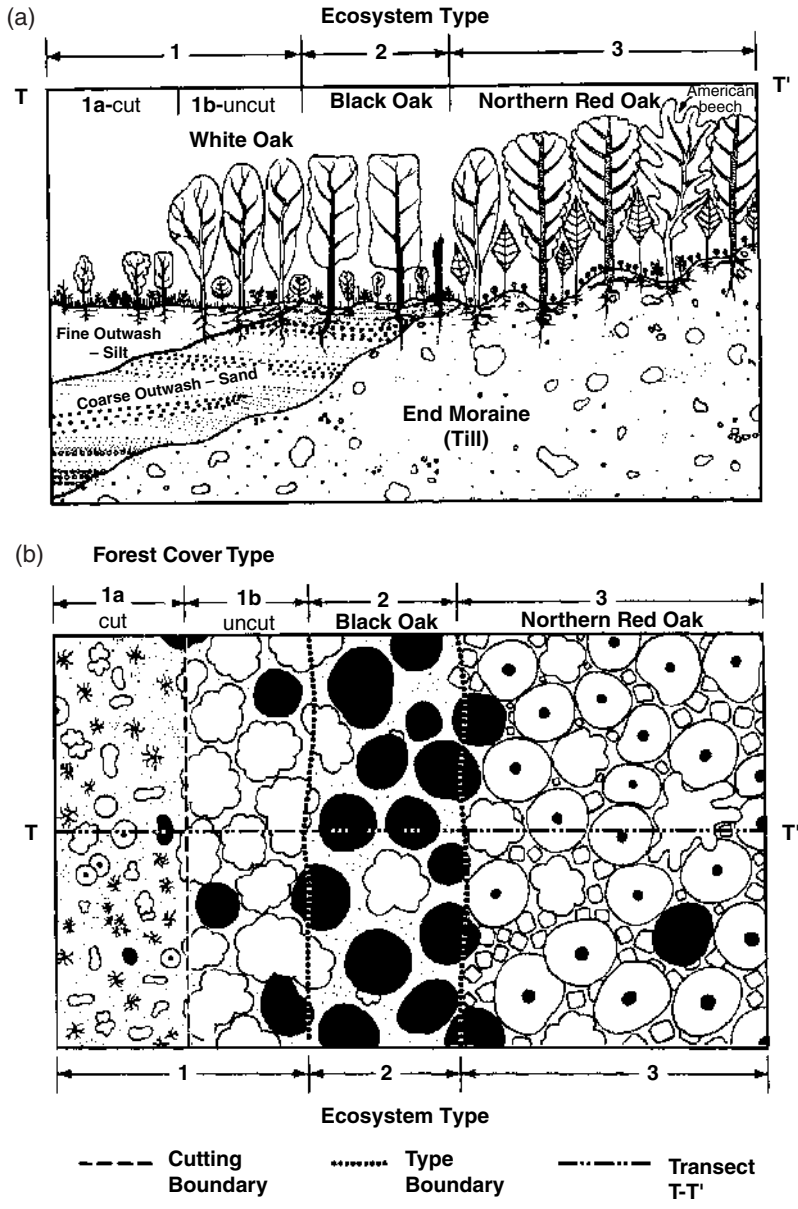

FIGURE 1.5 Three local *landscape ecosystem types* in glacial terrain that are differentiated by landform, parent material, soil, and vegetation: (a) Lateral transect from T to T′ showing vegetation and underlying geological parent material. (b) Top view showing distribution of forest trees, cover types, and ecosystem types. Following clear-cutting of part of type 1, two forest cover types (1a—early successional oak forest; 1b—old-growth white-oak forest) are distinguished. The diagram illustrates that different forest cover types (1a and 1b) are not necessarily different *ecosystem types*. They represent two of many possible ecosystem derivatives (disturbed in 1a versus relatively undisturbed in 1b) of a given ecosystem type. See text for discussion.

la). The overstory tree layer of the disturbed area is now dominated by white, black, and red oaks, white ash, black maple, American elm, black cherry, and sassafras. These species either sprouted from the base of cut trees, were already present in the white oak forest understory, or seeded in from adjacent communities following cutting. Today, we can recognize two (types 1a and 1b) of the many compositionally different forest communities that might occur at the site of ecosystem type 1; these easily could be mapped as two different forest cover types. Because the cut-over area (type 1a) has physiography and soil like type 1b, its vegetation may gradually become similar in structure to those of ecosystem type 1b, providing that no major changes in climate, soil, or ecosystem processes (including changed browsing pressure by herbivores) were caused by clear-cutting. Thus, a given local ecosystem type, defined by relatively stable features of physiography and soil, may have a suite of disturbance-induced cover types (Simpson et al. 1990). Therefore, recognizing forest cover types alone is not necessarily likely to provide a useful estimate of site potential for management or conservation. However, cover types are extremely useful in management planning for wildlife, timber, water, and recreational use of existing forest communities.

It is often the conspicuous forest cover type that receives our immediate attention. However, the enormous complexity of geographic space and changes in its component ecosystems through time require that major attention be directed to atmospheric, geologic, physiographic, and soil properties of forest landscapes. In summary, for every landscape, a combination of factors should be used to distinguish the pattern of local and regional landscape and waterscape ecosystems that have similar ecological potential in the long run. Understanding ecological units at multiple spatial scales (Chapters 2, 11, and 22) is needed to provide the basis for monitoring ecosystem change over time and for ecosystem management.

AN APPROACH TO THE STUDY OF FOREST ECOLOGY

This book presents the scope of forest ecology as having at least two major parts. The first is *analysis*: studying the details of ecosystem components (atmosphere, organisms, and Earth). The second part is *synthesis*: understanding the broad ecological framework within which ecosystem components are integrated. We therefore emphasize a "big picture" approach even as we discuss much smaller details of the organic and inorganic parts of ecosystems, their interactions, and the structure and function of entire ecosystems. The explicit separation and analysis of the biotic and physical parts of ecosystems are not realistic or desirable from an ecological perspective, but may serve as reasonable subdivisions to provide both analysis and synthesis. The sequence of presentation is (i) understanding forest ecosystems at multiple spatial scales, (ii) the variation, life history, and structure of the forest tree, (iii) the physical environment of forests, (iv) forest communities, (v) forest ecosystem dynamics, and (vi) the outlook for and consideration of future forests.

In Part 1 of this book, landscape ecosystems are the primary objects of interest, but we observe the importance of understanding spatial scale in examining them. Spatial scale influences the observations we make about ecosystems because ecological processes vary as spatial scale changes. Advances in hierarchy theory in ecology have helped us to understand ecosystems as volumetric segments of the ecosphere within which smaller volumetric units are nested.

In Part 2, we consider that the forest tree largely owes its appearance, rate of growth, and size to the environment in which it has grown throughout its life. In other words, the **phenotype**, the individual as it appears in the forest, is the product of the environment acting on its **genotype**, its individual genetic constitution. An understanding of trees as parts of ecosystems depends, in part, upon the genetics of the trees themselves and the way their genetic heritage affects their response to the environment they live in. In addition, life history features of regeneration as well as anatomical and physiological aspects of forest trees in relation to environment are considered.

We examine the physical factors of forest ecosystems in Part 3. The **site** is the sum total of environmental factors surrounding and available to the plant at a specific geographic place. These factors are primarily the atmospheric, physiographic, and soil components of the physical environment, but also include important influences of growing vegetation which itself affects the microclimate and soil. **Climate** includes various atmospheric factors that vary across hours, days, months, and years, such as solar radiation, air temperature, precipitation, humidity, wind, and carbon dioxide content. We provide special consideration to **sunlight** (solar radiation) and **temperature**, and we examine the relations and dynamics of **water** throughout the text in appropriate contexts. Physiological processes related to photosynthesis, respiration, and growth are included in Part 3 in chapters on light and temperature, but also in later chapters on carbon balance and nutrient cycling.

Physiography—comprising landforms and soil parent material——plays a key role in affecting climate as well as the amount and rates at which radiation and moisture are received and distributed in forest ecosystems. Below the ground surface, the supply of soil moisture and nutrients, the physical structure of the soil, microbial communities in the soil, and the nature and decomposition pattern of organic matter, that is, factors pertaining to **edaphic** characteristics of soil, all affect the growth and development of plants. We also treat fire as a site factor. The study of the environmental factors and their effects on individual plants constitutes the field of **autecology**, and we summarize those aspects of forest autecology most pertinent to an understanding of forest ecosystems. Finally, we examine site quality and its evaluation, focusing on the degree to which individual site factors and combinations of them are used to estimate the productivity of forest ecosystems and determine management prescriptions for them.

In Part 4, we consider forest communities and their plants and animals as integral parts of ecosystems. First, we examine the important roles of animals in affecting all phases of plant development, as well as their effects on forest communities and ecosystem processes. Forest communities are then treated, emphasizing their composition, occurrence, and the interactions (with emphasis on competition and mutualism) of their constituent individuals. Finally, we examine concepts of biological and ecological diversity, including their importance, measurement, and conservation.

Forest ecosystems are ever changing, and we examine their dynamics in Part 5. We first consider change in ecosystems over hundreds to millions of years. Primary bases for this change come from geologic and physiographic studies of the land itself and determination of plant species and their communities as deduced from the paleoecological record. Disturbance and succession as ecosystem processes are treated next, followed by chapters on whole ecosystem functioning, including the carbon balance of trees and ecosystems and the dynamics of nutrients.

Part 6 examines future forest ecosystems in considering their sustainability. We first examine the effects of climate change on forest ecosystems, including effects on individuals, populations, communities, and whole ecosystems. We also explore the potential for mitigation of climate change using forest management. We next consider the importance of invasive plants and animals for forest ecosystem structure and function. Finally, we place humans in an appropriate context of forest ecosystems in considering forest landscape ecology and the emerging concept of forest sustainability.

APPLICABILITY TO FOREST MANAGEMENT

The management of forests is, as it should be, a continuously evolving effort as new science, technology, and consideration of the role of humans in forest ecosystems develop. Management of forests may include decisions made at broad or local scales, but consideration is increasingly given to whole systems, their complexity and heterogeneity, as well as their long-term sustainability and integrity (Franklin et al. 2018) rather than single-focus use of their parts for recreation, wildlife, or

timber. To ecologists, understanding ecosystems for their own sake has significant value in itself, but the principles of forest ecology are essential for their guidance in conservation and management practices. Spurr (1945) defined **silviculture**, or applied forest ecology, as the theory and practice of controlling forest establishment, composition, and growth. Modern texts suggest that current silviculture is most concerned with managing forests for future products and services in a manner that has social stability (Ashton and Kelty 2018). Nevertheless, we explicitly emphasize that silviculture is the theory and practice of controlling forest ecosystem composition, structure, function, and heterogeneity, often at multiple spatial and temporal scales. Even local management operations may have significant and often long-term effects on surrounding landscapes far removed from the specific site of human activity.

The management, conservation, and restoration of forested landscape ecosystems rely heavily on understanding the structure and function of forest ecosystems and the autecology of their organisms (i.e., forest ecology). More than ever, understanding how ecological systems work is critical for making sound decisions regarding human intervention in forests. Understanding the structure and function of whole ecosystems will also equip us to best deal with the ecological consequences of past human activities, such as deforestation and its wide range of impacts, habitat loss, and fragmentation. Human activities associated with industrialization, such as air pollution or the introduction of destructive new species, have resulted in local tree mortality and, in certain ecosystems, widespread death and decline of forest trees and other organisms. Increasing the carbon dioxide concentration in the atmosphere due to the burning of fossil fuels and deforestation are creating climatic changes and concomitant changes in forest ecosystems that are quickly increasing in their severity. Invasive plants and animals introduced into forests are well known for disrupting ecosystem structure and function on relatively short time scales. In all cases, one must understand the system in order to understand the extent to which it is disrupted.

At the time of the last edition of this textbook over 20 years ago, a new paradigm in forestry had occurred that shifted the view of the forest from one of single commodities (timber, wildlife, water, and recreation) to forestry understood as sustaining ecosystems and their structure, diversity, heterogeneity, and function (Rowe 1994; Kohm and Franklin 1997). That paradigm emphasized maintaining the integrity of ecosystems across landscapes by sustaining their natural patterns and processes even when heavily manipulated by humans. This paradigm has been further refined over the past two decades to include an emphasis on considering or even incorporating natural disturbances, increasing ecosystem resistance and resilience, embracing structural complexity, and maintaining a range of ecosystem conditions across broad scales (Franklin et al. 2018). Whether intentionally or otherwise, this paradigm has the landscape ecosystem approach at its core because it focuses on the maintenance of landscapes *as complete ecosystems*. The only way to assure the sustained yields of forests, wildlife, and water, now and in the future, is to maintain the integrity of their processes and keep their biota in a healthy state. Such a practice demands an intimate familiarity with forest ecology as we have described it.

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