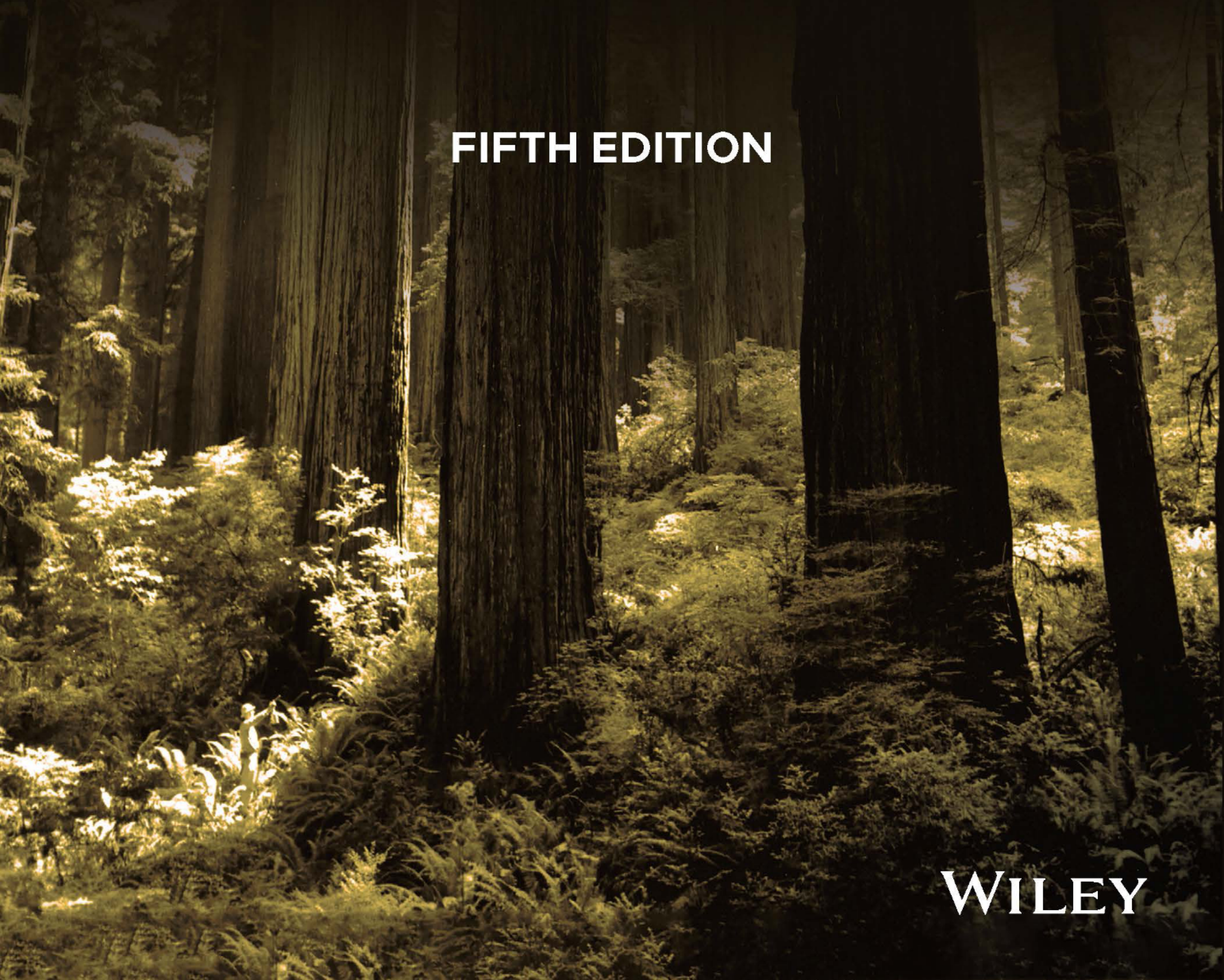
FOREST ECOLOGY

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

FIFTH EDITION



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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