1
Ecosystem Function in Heterogeneous Landscapes

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Introduction

The ecosystem concept has been a powerful tool in ecology, as it allows the use of the quantitative and rigorous laws of conservation of mass and energy in the analysis of entire ecological systems. These laws require delimiting an ecosystem by specifying its boundaries; however, we know that these boundaries are porous and that all ecosystems are open systems that exchange matter, energy, information, and organisms with their surroundings. This openness means that ecosystems defined as spatially separate are in fact interconnected parts of a larger landscape. Once we begin to ask about the source of the inputs or the fate of the outputs, we need to consider the ecosystem in its landscape context.

The role of landscape context in ecosystem functioning has historically received rather short shrift, and we believe the subject is ripe for synthesis and conceptual progress. Consequently, the goal of this book is to focus the attention of the ecosystem science research community on how interactions among ecosystems affect the functioning of individual ecosystems and the larger landscape in which they reside. This subject is becoming increasingly important as ecosystem scientists are being asked to provide information on environmental problems at local, regional, and global scales—a task that cannot be accomplished by examining ecosystems in isolation. Fundamentally, the problem of scaling up from individual ecosystems to larger spatial scales depends on how we conceptualize heterogeneity in a landscape composed of multiple, potentially interacting ecosystems.

This book is an outgrowth of the Tenth Cary Conference, held April 29–May 1, 2003, in Millbrook, New York. As with all Cary Conferences, this conference focused on a difficult conceptual and practical problem in ecosystem science and brought together leading thinkers and practitioners to offer different perspectives and try to advance understanding of the issue. This book brings the same approach to print. It reflects the challenges and problems identified by the participants in the conference as well as different perspectives on solutions to those problems, both conceptual and practical.

Although ecosystem ecology has focused on ecosystem function, particularly the flows of mass and energy, the spatial structure of landscapes has largely been the province of landscape ecology. Historically, landscape ecologists have tended to focus on the quantification of landscape structure, often to understand its influence on animal movement, population persistence, or disturbance dynamics. It is only recently that landscape ecologists have begun to consider other ecosystem processes such as mass and energy transfer. Thus, in some ways, this book is a bridge between ecosystem and landscape ecology, encompassing both the landscape ecologists' knowledge of spatial structure and the ecosystem ecologists' knowledge of system function. In this book, we take a broad view of the term *landscape*, with no particular spatial scale implied, and we include heterogeneous aquatic as well as terrestrial systems.

We embarked on this project knowing full well that the existence of spatial heterogeneity would not be a startling revelation to ecologists. Heterogeneity is everywhere, and most ecosystem ecologists deal with it on a daily basis in designing their experiments and analyzing their data. Sometimes, ecologists use heterogeneity as a tool, such as when we contrast riffles and pools in a stream or forests on different soil types. Other times, we see spatial heterogeneity as noise obscuring the pattern we wish to observe. Accounting for spatial heterogeneity in ecosystem processes costs us dearly in time, money, and statistical agony. The goal of this book is to move beyond the quantification and description of heterogeneity to understand when it matters to ecosystem function and when it does not. When can we ignore it, when should we deal with it, and, if we need to deal with it, what are the best conceptual tools for doing so?

Concepts and Definitions

A few key concepts recur throughout the book and require some introduction. First, many of the chapters refer to a scheme for organizing different approaches to spatial heterogeneity proposed by Shugart (1998). Shugart discussed modeling approaches for terrestrial ecosystems, which he classified as "homogeneous," meaning no spatial heterogeneity is represented; "mosaic," meaning that spatial heterogeneity is present in that different spatial units in the model have different characteristics, but there is no interchange between the units; and "interactive," meaning that spatial units are distinct and exchange mass, energy, organisms, or information with one another (Figure 1.1). We found this a useful way to categorize general conceptual approaches to heterogeneity, and this terminology appears repeatedly in the book, beginning with Chapter 2 by Turner and Chapin. Our goal was to understand the circumstances under which each of these approaches is appropriate.

A second concept that occurs throughout the book is that of compositional versus configurational heterogeneity. Compositional heterogeneity refers to the number, type, and abundance of spatial units in the landscape, whereas configurational heterogeneity refers to the spatial arrangement of those units.

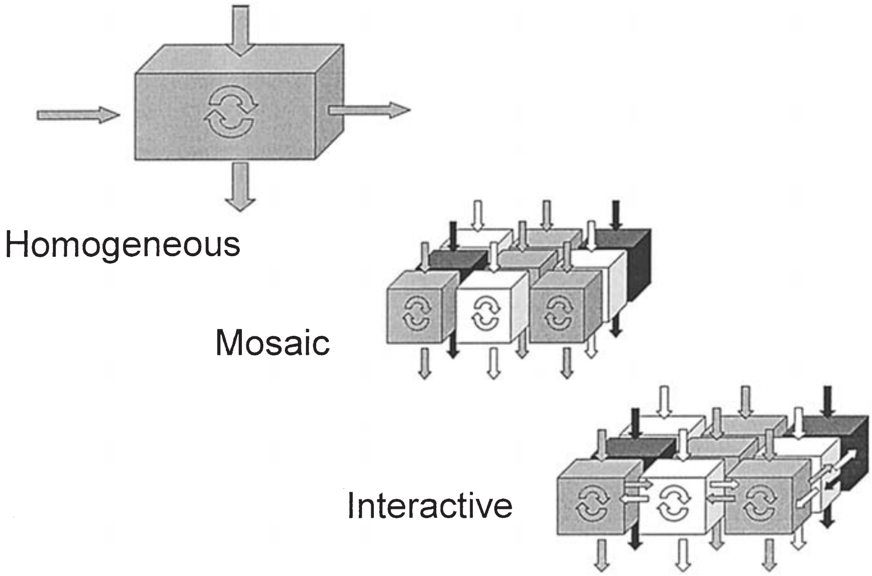

FIGURE 1.1. Schematic representation of three conceptual approaches to heterogeneity. Classification follows Shugart (1998).

A third concept concerns the representation of heterogeneity in data and models. In some cases, heterogeneity is expressed in discrete units, usually called patches. In other cases, heterogeneity is expressed as continuous variation across the landscape; if this variation is monotonic, it is called a gradient. There is also a middle ground between these two end-points, for instance "neighborhood" models in which the properties of a given patch are influenced by its surroundings and the influence often declines with distance from the focal patch, and "networks," which are hierarchically arranged, interconnected series of patches (see White and Brown, Chapter 3).

Finally, there are a number of terms used in the book that may cause confusion because they have different meanings to different people. In an effort to minimize semantic confusion, we have defined several important terms in Table 1.1. These definitions are not meant to be restrictive; rather, they represent what we consider the most common usage of these terms. We asked the authors to make it clear in their papers if they used any of these terms differently.

Organization of the Book

The book has five sections. Section I ("Challenges and Conceptual Approaches") contains four chapters that describe the problem of dealing with spatial heterogeneity in ecosystem science and offer conceptual

TABLE 1.1. Definitions of Some Commonly Used Terms in the Book

Configuration: A specific spatial arrangement of elements or entities (biotic or abiotic); often used synonymously with spatial structure or patch structure.
Connectivity: The spatial continuity of an entity or function.
Ecosystem: A spatially explicit unit of the earth that includes all of the organisms, along with all components of the abiotic environment, within its boundaries.
Ecosystem Function: Attribute related to the performance of an ecosystem that is the consequence of one or of multiple ecosystem processes. Examples include nutrient retention, biomass production, and maintenance of species diversity.
Ecosystem Process: Transfer of energy, material, or organisms among pools in an ecosystem. Examples include primary production, decomposition, heterotrophic respiration, flux and cycling of elements, and evapotranspiration.
Gradient: Change in a property across a defined spatial extent.
Heterogeneity: The quality or state of encompassing variation in a property of interest, as with mixed habitats or environmental gradients occurring on a landscape; opposite of homogeneity, in which variation in the property is negligible.
Landscape: An area that is spatially heterogeneous in at least one factor of interest.
Patch: A surface area that differs from its surroundings in structure or function.
Scale: Spatial or temporal dimension of an object or process, characterized by both grain and extent.

frameworks to help address the problem. Section II ("Perspectives from Different Disciplines") has four chapters that explore various conceptual and modeling approaches used in other spatial disciplines, specifically population biology, hydrology, epidemiology, and oceanography. Section III ("Illustrations of Heterogeneity and Ecosystem Function") contains seven chapters that treat the role of spatial heterogeneity in a diverse assortment of landscapes, such as arid systems, lakes, and boreal forests, with specific attention to the fundamental issues of what causes spatial heterogeneity, and when it does—and does not—matter for the functioning of the ecosystem or landscape. Section IV ("Application of Frameworks and Concepts") consists of three chapters that treat the need for knowledge about spatial heterogeneity in practical resource management issues pertaining to fire, water, and the design of biological reserves. In the final section, (Section V, "Synthesis"), five chapters (including a final chapter by the editors) tie together the various threads of the book, providing synthetic views of the problem and describing progress in developing overarching conceptual frameworks.

Reference

Shugart, H.H. 1998. Terrestrial ecosystems in changing environments. Cambridge, UK: Cambridge University Press.