Ecosystem Function in Heterogeneous Landscapes

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With 96 Illustrations

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Foreword

Among the most difficult problems in the life sciences is the challenge to understand the details of how ecosystems/watersheds/landscapes function. Yet, the welfare of all life, not just the human species, depends upon the successful functioning of diverse and complicated ecosystems, each with various dimensions and compositions. Central to this "working" is the dominance, and to a major extent control, of ecosystems by organisms, which means that these systems are constantly changing as the component organisms change and evolve. Such changes increase the challenge to understand the functioning of ecosystems and landscapes. Moreover, understanding the interactions among the myriad components of these systems is mind-boggling as there are scores of biotic (probably many thousands of species when the microbial components are fully enumerated through genomics) and countless abiotic (ions, molecules, and compounds) entities, all simultaneously interacting and responding to diverse external factors to produce functional or dysfunctional environments for life.

This book focuses on the problems of connectedness and ecosystem functioning. It is difficult enough to understand how an ecosystem functions when it is considered in isolation, but all ecosystems are open and connected to everything else. Clearly, the inputs to any ecosystem are the outputs from others and vice versa, and as such the fluxes represent major, if not critical, points for managing or changing the overall functioning of an ecosystem or landscape. A major challenge is to find appropriate conceptual frameworks to address these complicated problems. Understanding spatial heterogeneity is now recognized as one of the most significant aspects of this challenge. However, because ecologists have ignored spatial heterogeneity for so long, there is a pressing need to integrate it into their studies, theories, and models. With new frameworks and tools, ecology is now poised to make important strides forward in the focused study of heterogeneity from an ecosystem and landscape perspective. Ecology has accepted the challenge of understanding these complicated systems overall, and is making good progress toward doing so. Such knowledge is vital to guide conservation initiatives, sustainable management, mitigation of environmental impacts, and future breakthroughs in understanding.

With funding from The Andrew W. Mellon Foundation, the Institute of Ecosystem Studies (IES) launched a study of "*Ecosystem Function in Mosaic Landscapes: Boundaries, Fluxes, and Transformations*" in 1999. We proposed that our research would advance the understanding of how heterogeneity influences ecosystem function by:

"1) rigorously assess[ing] the degree of ecosystem heterogeneity at different scales . . .;
2) determin[ing] how ecosystem heterogeneity affects long-term change in the mosaics of which they are a part;
3) focus[ing] on the role of boundaries between and within ecosystems in governing ecosystem function; and
4) discover[ing] how fluxes across mosaics affect the organismal, material, and energetic transformations [within and among] ecosystems."

The 2003 Cary Conference, "Ecosystem Function in Heterogeneous Landscapes," addressed many of these challenges and the results are brought together in this book. Cary Conferences, started at IES in 1985, have identified and addressed such major "cutting edge" questions and challenges in an effort to provide leadership in the field. This Conference was no exception.

With the leadership of Drs. Lovett, Jones, Turner, and Weathers, the authors of this volume have brought their diverse talents and experiences to bear on the topic of how interactions among ecosystems affect not only their own functioning, but the function of the larger landscape or region in which they are embedded, and have done so in new and enlightened ways. By evaluating the linkages at different scales, the authors of this volume have progressed toward building the "suspension bridge" between ecosystem and landscape ecology, a major goal of the editors of this volume.

There is an important need for revised models, conceptual as well as mechanistic, that will allow ecologists to bring the many aspects of heterogeneity together under one framework. As ecologists continue to develop these new frameworks for understanding how ecological systems function, the ideas put forward in this book hopefully will catalyze new studies that will lead to a more synthetic and unified understanding of heterogeneity, and in the process, a greater understanding of how ecosystems and landscapes "work."

Gene E. Likens
President and Director
Institute of Ecosystem Studies
July 2005

Acknowledgments

This book is an outcome of the Tenth Cary Conference held at the Institute of Ecosystem Studies (IES) in Millbrook, NY, April 29-May 1, 2003. Many people helped to make the conference a success, and we sincerely appreciate their efforts. In particular, we are grateful to all the conference participants for contributing the ideas and enthusiasm that made the conference exciting and intellectually challenging. The conference Steering Committee–Lenore Fahrig, Timothy Kratz, and Gene Likens–provided important guidance in the development of the conference program. Our IES Advisory Committee, consisting of Peter Groffman, Michael Pace, Steward Pickett and David Strayer, generously lent their insight and experience from past Cary Conferences to the planning of this one. The entire staff of IES worked together to make the conference run smoothly and to provide a relaxed and stimulating atmosphere for the participants. Eight graduate students—Brian Allen, Darren Bade, Olga Barbosa, Jennifer Fraterrigo, Noel Gurwick, Jay Lennon, Michael Papaik, and Katie Predick—provided logistical support throughout the conference and conveyed their enthusiastic and upbeat attitude to all the participants. Most importantly, our Conference Coordinator, Claudia Rosen, provided us with her organizational talent, unflappable personality, style and good humor. It is because of her efforts that we were able to focus on the science and trust that the myriad problems of conference organization were solved behind the scenes; we thank her sincerely for that.

This book is, in many ways, a separate effort, and numerous individuals generously provided assistance. We thank the authors of the chapters for gamely taking on the broad subject areas assigned to them, giving excellent presentations at the conference, tolerating our nagging, and producing thoughtful and stimulating papers. We appreciate the effort and insight provided by the reviewers of the chapter manuscripts, who provided excellent advice on a demanding schedule. We are especially grateful to the organizations that provided financial support for both the conference and the book, including the National Science Foundation (through grant DEB0243867), The USDA Forest Service, the Environmental Protection Agency, the A.W. Mellon Foundation, and the Institute of Ecosystem Studies.

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1
Ecosystem Function in Heterogeneous Landscapes

Gary M. Lovett, Clive G. Jones, Monica G. Turner, and Kathleen C. Weathers

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.

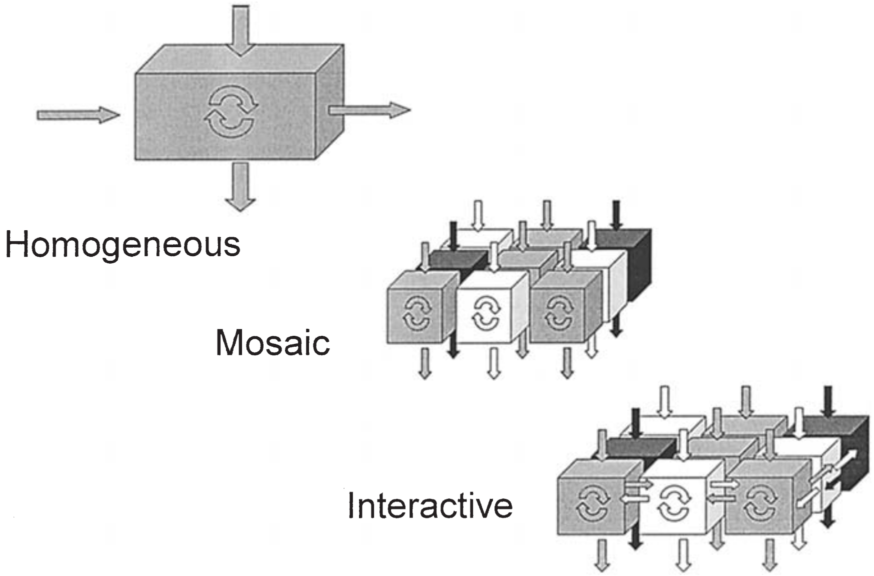

FIGURE 1.1. Schematic representation of three conceptual approaches to heterogeneity. Classification follows Shugart (1998).

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.

Section I

Challenges and Conceptual Approaches

Editors' Introduction to Section I: Challenges and Conceptual Approaches

The first step toward building a complete understanding of landscape heterogeneity and ecosystem function is to develop a conceptual framework and identify the challenges that need to be overcome. This is no simple task. There are many interactions between spatial heterogeneity and ecosystem processes that occur on multiple temporal and spatial scales; how to structure our thinking in a way that promises new insights is not readily apparent. This first section of the book offers four different perspectives that address this daunting topic, perhaps suggesting some of the structural elements needed for a solid framework.

Monica Turner and Terry Chapin (Chapter 2) briefly describe the background of research on spatial heterogeneity and ecosystem function in both ecosystem and landscape ecology. They introduce the concepts of point processes and lateral transfers to describe situations in which horizontal movement between units in a landscape is or is not important, respectively. They discuss ways of conceptualizing heterogeneity (homogeneous, mosaic, and interactive models) and offer insights to when spatial heterogeneity may be important in ecosystem studies. This chapter presents the basis of a conceptual framework that allows ecologists to sort out when heterogeneity may be important to consider.

Ethan White and Jim Brown (Chapter 3) consider the template upon which ecosystems function and begin by posing the question, "How and why is the landscape heterogeneous?" They argue that it is necessary to have a quantitative understanding of heterogeneity before its functional importance can be understood, and they present three general categories (gradients, patches, and networks) of environmental heterogeneity. They further suggest that these different types of spatial heterogeneity reflect different causal mechanisms, and they illustrate these with selected examples. This chapter offers a conceptual and mathematical framework for characterizing patterns of heterogeneity and understanding the processes underlying those patterns.

In Chapter 4, John Pastor focuses on three processes that generate pattern in the landscape: physical disturbance, directional transport of energy and materials, and diffusive instability. He discusses both the conceptual basis and the mathematical modeling of these phenomena, using many chapters from this book as case studies.

Bill Reiners (Chapter 5) offers a very general and comprehensive conceptual framework for understanding the transport of mass, energy, organisms, and information on the landscape. He discusses how these transport phenomena are influenced by spatial heterogeneity and how in turn heterogeneity alters the transport. This conceptual framework should be particularly helpful for developing models of fluxes between ecosystems on a landscape, as it describes the fundamental concepts behind transport phenomena.

2
Causes and Consequences of Spatial Heterogeneity in Ecosystem Function

Monica G. Turner and F. Stuart Chapin III

Abstract

Understanding the causes and consequences of spatial heterogeneity in ecosystem function represents a frontier in both ecosystem and landscape ecology. Ecology lacks a theory of ecosystem function that is spatially explicit, and there are few empirical studies from which to infer general conclusions. We present an organizing framework that clarifies consideration of ecosystem processes in heterogeneous landscapes; consider when spatial heterogeneity is important; discuss methods for incorporating spatial heterogeneity in ecosystem function; and identify challenges and opportunities for progress. Two general classes of ecosystem processes are distinguished. *Point processes* represent rates measured at a particular location; lateral transfers are assumed to be small relative to the measured response and are ignored. Spatial heterogeneity is important for point processes when (1) the average rate must be determined over an area that is spatially heterogeneous or (2) understanding or predicting the spatial pattern of process rates is an objective, for example, to identify areas of high or low rates, or to quantify the spatial pattern or scale of variability in rates. *Lateral transfers* are flows of materials, energy, or information from one location to another represented in a two-dimensional space. Spatial heterogeneity may be important for understanding lateral transfers when (1) the pattern of heterogeneity influences net lateral transfer and potentially the behavior of the whole system, (2) the spatial heterogeneity itself produces lateral transfers, or (3) the lateral transfers produce or alter patterns of spatial heterogeneity. We discuss homogeneous, mosaic, and interacting element approaches for dealing with space and identify both challenges and opportunities. Embracing spatial heterogeneity in ecosystem ecology will enhance understanding of pools, fluxes, and regulating factors in ecosystems; produce a more complete understanding of landscape function; and improve the ability to scale up or down.

Introduction

Understanding the causes and consequences of spatial heterogeneity in ecosystem function represents a frontier in both ecosystem and landscape ecology (Turner et al. 2001; Chapin et al. 2002), and it is recognized as important in a variety of other disciplines; for example, biological oceanography (Platt and Sathyendranath 1999), limnology (Soranno et al. 1999), soil ecology (Burke et al. 1999), conservation (Pastor et al. 1999), and global change studies (Shugart 1998; Canadell et al. 2000). Ecosystems do not exist in isolation, and interactions among patches on the landscape influence the functioning of individual ecosystems and of the overall landscape. Efforts to estimate the cumulative effect of ecosystem processes at regional and global scales have contributed to the increased recognition of the importance of landscape processes in ecosystem dynamics (Chapin et al. 2002). Transfers among patches, representing losses from donor ecosystems and subsidies to recipient ecosystems, are important to the long-term sustainability of ecosystems (Polis and Hurd 1996; Naiman 1996; Carpenter et al. 1999; Chapin et al. 2002).

Ecology lacks a theory of ecosystem function that is spatially explicit, and there are few empirical studies from which to infer general conclusions. Ecosystem ecology focuses on the flow of energy and matter through organisms and their environment. As such, it addresses pools, fluxes, and regulating factors. Spatially, ecosystem ecology encompasses bounded systems like watersheds, spatially complex landscapes, and even the biosphere; temporally, it crosses scales ranging from seconds to millennia (Carpenter and Turner 1998). From its initial descriptions of the structure and function of a diverse variety of ecosystems, ecosystem ecology moved toward increasingly sophisticated analyses of function; for example, food web analyses, biogeochemistry, regulation of productivity, and so forth (Golley 1993; Pace and Groffman 1998; Chapin et al. 2002). Typically, ecosystem studies are conducted within a single ecosystem, such as a lake or a forest stand, and homogeneous sites are generally chosen to minimize the complications associated with spatial heterogeneity. From ecosystem studies, ecology has gained an excellent understanding of the mechanisms underlying many processes and of temporal dynamics in function. However, understanding patterns, causes, and consequences of spatial heterogeneity in ecosystem function remains a frontier.

Landscape ecology explicitly addresses the importance of spatial configuration for ecological processes (Turner et al. 2001), and, in North America, landscape studies were strongly promoted by ecosystem ecologists (Risser et al. 1984). Landscape ecology often, but not always, focuses on spatial extents that are much larger than those traditionally studied in ecosystem ecology. Early research in landscape ecology emphasized methods to describe and quantify spatial heterogeneity, spatially explicit models to relate pattern and process, and understanding of scale effects. Indeed, there