Monica G. Turner
Robert H. Gardner

Landscape Ecology in Theory and Practice

Pattern and Process

Second Edition

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Monica G. Turner
University of Wisconsin-Madison
Department of Zoology
Madison, WI, USA

Robert H. Gardner
University of Maryland
Center for Environmental Science
Frostburg, MD, USA

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DEDICATION

Frank B. Golley: Scholar, Mentor, Friend

There are people whom we encounter in life who make a real difference. They may influence us as individuals by their encouragement and guidance; they may affect their community through their untiring commitment to service and the greater good; or they may influence an entire profession by their scholarship, leadership, and example. We dedicate this second edition of *Landscape Ecology in Theory and Practice* to Frank B. Golley (1930–2006) who made a real difference in all of these ways. Frank spent most of his career at the University of Georgia and was Monica's graduate advisor. We marked his many accomplishments previously (see Turner et al. 2007, *Landscape Ecology* 22:1–3) but note here his service as founding editor of *Landscape Ecology*, president of the Ecological Society of America and the International Association for Ecology (INTECOL), and director of the Biological Sciences Directorate at the National Science Foundation. But beyond his many academic achievements and the lasting influence he had on the development of landscape ecology, Frank was a wonderful person, a mentor, and friend who touched both of us deeply. We would not be where we are today without him. We thank him for all that he gave of himself, and we still mourn his loss. Frank, this is for you.

PREFACE TO THE SECOND EDITION

Heterogeneity, pattern, process, scale, and hierarchy are intrinsically interrelated concepts … key to the theory and practice of landscape ecology. Wu (2013)

The literature of landscape ecology has expanded tremendously since the first edition of *Landscape Ecology in Theory and Practice* was finished in early 2000. Indeed, the number and diversity of published landscape studies is staggering. It is wonderful that the field has blossomed, but synthesizing the advancements and literature of landscape ecology has been a very daunting task. Nonetheless, we have tried to capture key developments in the field, but we also recognize that this goal will probably be met only partially. Despite a large bibliography with well over 1000 references cited, there was no way to include all studies. By necessity, our examples and citations are illustrative, not comprehensive.

How is the second edition organized, and in what ways does it differ from the first edition? The first two chapters set the stage. Chapter 1 (*Introduction to Landscape Ecology and Scale*) introduces the field of landscape ecology and reviews its intellectual foundations, and it now includes a basic introduction to scale concepts and terminology. Scale remains important, but we no longer felt it required a stand-alone chapter; however, scale issues infuse the rest of the book. Chapter 2 (*Causes of Landscape Pattern*) has been much enhanced. Treatment of multiple and contingent causation is much expanded, along with the challenges associated with forecasting future landscape patterns in the context of multiple changing drivers.

Landscape development and landscape legacies are also treated in greater depth, reflecting advances in understanding of how land-use history affects contemporary landscapes.

After setting the stage, three chapters deal with quantitative methods in landscape ecology. These analysis methods are key tools for scholars and practitioners in landscape ecology and the means to the end in many studies. Chapter 3 (*Introduction to Models*) focuses on simulation modeling, providing an overview of spatially explicit landscape models, which are used widely in landscape ecology. Chapter 3 also presents neutral landscape models (NLMs), which were instrumental in early quantitative studies of pattern–process relationships. Some readers (especially those who are new to spatial pattern analysis) may prefer to read Chaps. 4 and 5 *before* reading Chap. 3. Chapter 4 (*Landscape Metrics*) covers the range of landscape metrics used with categorical data, including metrics calculated for the entire landscape and by cover type or patch. This chapter has been updated to introduce some newer approaches, but as in the past, it emphasizes proper use and interpretation of metrics rather than exhaustive coverage. Chapter 5 (*Spatial Statistics*) is new and was needed because of substantial advances in methods for analyzing spatial dependence in continuous data, and their wide use.

With the foundation established and quantitative methods presented, the next three chapters deal with particular pattern–process relationships. All three chapters have been substantially revised and updated to reflect the growth of knowledge in these areas. Chapter 6 (*Disturbance Dynamics*) now includes new topics such as landscape epidemiology and disturbance interactions. Chapter 7 (*Organisms and Landscape Patterns*) was extended to cover interactions among species, community structure, species invasions, and landscape genetics. Each of these topics has seen tremendous progress in the past 15 years. Chapter 8, *Ecosystem Processes in Heterogeneous Landscapes*) distinguishes between ecosystem processes characterized primarily by vertical fluxes and processes that represent lateral transfers.

The last two chapters consider applications and synthesis. Chapter 9 (*Landscape Dynamics in a Rapidly Changing World*) deals with applications of landscape ecology and has been thoroughly revised. This chapter now considers landscape indicators, climate change, and landscape sustainability, in addition to an expanded treatment of land-use change and landscape scenarios. The final and relatively brief chapter (*Conclusions and Future Directions*) summarizes key lessons from landscape ecology and directions for future research.

Acknowledgements

Research that we have conducted over the past 15 years has contributed to the writing of this book. Turner especially acknowledges research funding in support of this effort from the National Science Foundation, including the Long-Term Ecological Research Program (Coweeta LTER: DEB-0823293 and North Temperate

Lakes LTER: DEB-0822700) and Water Sustainability and Climate Program (DEB-1038759); the Joint Fire Science Program (Grants 09-1-06-3, 09-3-01-47, 11-1-1-7); the Andrew W. Mellon Foundation; the Department of Zoology and Graduate School of the University of Wisconsin-Madison; and the Wisconsin Department of Natural Resources.

Turner thanks all the students and postdocs who have been part of my lab for many spirited and fun discussions about landscape ecology; I learn so much from you. I especially thank my recent lab members Pete Blank, Dan Donato, Catherine Frock, Rose Graves, Winslow Hansen, Brian Harvey, Jiangxiao Qiu, Kevin Rose, Amy Uhrin, Tim Whitby, and Carly Ziter, not only for their input but also their understanding when I have absented myself to write. My ideas and understanding of landscape ecology have also benefitted from long-term collaborations with valued colleagues, especially Bill Romme and Scott Pearson, and the outstanding group of excellent ecologists at the University of Wisconsin-Madison. Graduate students in my Advanced Landscape Ecology course at UW-Madison have been a tremendous source of inspiration and new knowledge. I also thank Sarah Gergel for her hard work and perseverance to complete the second edition of *Learning Landscape Ecology*, which makes a great companion to this text and offers many options for hands-on learning of the approaches we describe here.

Gardner thanks the faculty, staff, and students of the Appalachian Laboratory for their generous support and enthusiasm during the development of this new edition. Special thanks are due Katia Engelhardt, Andrew Elmore, and Matt Fitzpatrick for stimulating discussions, collaboration, and assistance in teaching landscape ecology. None of this would be possible without the love and support of wife, Kim S. Gardner, and family. The University of Maryland Center for Environmental Science (UMCES) is a unique institution of which the Appalachian Laboratory is a part. Faculty and students of other UMCES labs, especially the Horn Point Laboratory and Chesapeake Biological Laboratory, provided a stimulating environment for vetting concepts and ideas with particular thanks to Michael Kemp and Walter Boynton who listened critically and freely offered new ideas. The direct support provided by the UMCES and by the National Science Foundation grant DEB 0841394 is greatly appreciated.

We also recognize Bob O'Neill for his contributions to the first edition and for many great years of collaborative research at Oak Ridge National Laboratory (ORNL). At the time when landscape ecology developed rapidly in North America, we were fortunate to have been a part of exciting collaborations with Bob and others at ORNL. We are grateful to Janet Slobodien, our editor at Springer, for her patience, as it has taken longer than anticipated to complete the book. Finally, we thank friends and colleagues for constructive comments on various chapters, including Inger Auestad, Pete Blank, Jeff Cardille, Cat Frock, Sarah Gergel, Rose Graves, Winslow Hansen, Brian Harvey, Stein Hegland, Marte Lilleeng, Jiangxiao

Qiu, Dean Urban, and Carly Ziter. Comments from Brian Harvey improved the discussion questions that complete each chapter. Many other colleagues graciously shared digital photographs or figure files. As with the first edition, the graphics and illustrations for this book were prepared by Michael Turner. Producing the graphics was a major effort that required generating new figures and also updating formats and increasing resolution for all figures, and this consumed months of weekends. We thank him for enhancing the visual content of this book, bringing color and consistency into all of the illustrations, and improving communication of our content with his careful attention to aesthetics. Finally, we thank our families for their understanding of the many hours we have spent working on this revision over several years.

Monica G. Turner
Madison, WI

Robert H. Gardner
Santa Rosa, CA

June 2015

PREFACE TO THE FIRST EDITION

Landscape ecology is not a distinct discipline or simply a branch of ecology, but rather is the synthetic intersection of many related disciplines that focus on the spatial-temporal pattern of the landscape.

Risser et al. (1984)

The emergence of landscape ecology as a discipline has catalyzed a shift in paradigms among ecologists, … resource managers and land-use planners. Having now seen the faces of spatial pattern and scale … we can never go back to the old ways of viewing things.

Wiens (1999)

This book presents the perspective of three ecologists on the concepts and applications of landscape ecology—a discipline that has shown expansive growth during the past two decades. Although landscape ecology is a multidisciplinary subject involving components as diverse as economics and sociology, the earth sciences and geography, remote sensing and computer applications, we focus here on what ecologists need to know about landscapes.

Landscape ecology served as the integrating theme of our collaborative research for nearly 15 years, including a 7-year period during which we worked together at Oak Ridge National Laboratory (ORNL). We became acquainted in January 1986 at the first annual United States Landscape Ecology symposium held at the University of Georgia and organized by Monica Turner and Frank Golley. Landscape ecology was, at that time, a new subject in the USA. The first US workshop on landscape ecology, organized by Paul Risser, Richard Forman, and Jim Karr, had occurred less than 3 years prior (Risser et al. 1984). One of us (O'Neill) was a participant in that workshop, and two of us (O'Neill and Gardner) were research scientists in the Environmental Sciences Division of Oak Ridge National

Laboratory (ORNL) who had collaborated for several years on many aspects of ecosystem ecology and ecological modeling. Turner had a newly minted Ph.D. and was continuing as a postdoctoral research associate at the University of Georgia, where Frank Golley (also a participant at the 1983 workshop and Turner's Ph.D. advisor) was actively engaging his colleagues in the developing ideas in landscape ecology. The mutual interests shared by Turner, Gardner, and O'Neill, coupled with the excitement and challenge of working in a newly emerging branch of ecology, led to Turner's move to ORNL in July 1987. The subsequent 7 years in which we collaborated so closely were among the most exciting times that any of us have had in our careers. There are times and places at which creativity seems to be fostered more than others, and that time and place had it. The writing of this book was precipitated, in part, by the fact that although we are now located at different institutions, we shared the desire to provide a synthesis of the field in which we have worked so closely together.

As ecologists embraced the challenges of understanding spatial complexity, landscape ecology moved from being a tangential subdiscipline in the early 1980s to one that is now mainstream. Indeed, a landscape approach, or the landscape level, is now considered routinely in all types of ecological studies. It is our hope that this text will provide a synthetic overview of landscape ecology, including its development, the methods and techniques that are employed, the major questions addressed, and the insights that have been gained. The companion volume (Gergel and Turner 2000) provides opportunities for "hands on" learning of many of the methods and concepts employed by landscape ecologists. It is our hope that our books might serve to inspire others to embark on landscape ecological studies, for there is much yet to be learned. As we begin this new century, we look forward to the many contributions that landscape ecologists will make in the future and to the continued growth of this exciting discipline.

Acknowledgements

Research that we have conducted over the past 15 years and that lead to the development of this book has been funded by a variety of agencies, and we gratefully acknowledge research support from the National Science Foundation (Long-Term Ecological Research, Ecosystem Studies, and Ecology Programs), Department of Energy, USDA Competitive Grants Program, National Geographic Society, Environmental Protection Agency (EMAP and STAR programs), and the University of Wisconsin-Madison Graduate School.

Our ideas have evolved over the years and been shaped by fruitful, and often spirited, discussions with many colleagues. Among the most memorable of these were discussions with Don DeAngelis, Jeff Klopatek, John Krummel, and George Sugihara in the "pre-landscape" years at ORNL that crystallized much of the philosophy and approach adopted in our research. Virginia Dale, Kim With, Scott Pearson, and Bill Romme have been regular collaborators as well as supportive friends. Although it is impossible to mention everyone at ORNL that contributed ideas and assisted us with their expertise, we would be remiss not to acknowledge the valuable contributions of Steve Bartell, Antoinette Brenkert, Carolyn Hunsaker, Tony King, and Robin Graham. While at Oak Ridge we hosted a number of visitors from other institutions, including Bill Romme, Linda Wallace, Bruce Milne, Tim Kratz, Sandra Lavorel, Tim Allen, Eric Gustafson, and Roy Plotnick. Those colleagues made substantial contributions to and lasting impacts on our ideas, and we thank them all for engaging interactions and fruitful collaborations.

Special thanks are due to Richard Forman, Frank Golley, and John Wiens for long-standing collegial relationships, the sharing of their ideas (and students!) that often challenged our thinking, and their invaluable reviews and critiques over the years. Turner also sincerely thanks Hazel Delcourt (University of Tennessee) and David Mladenoff (University of Wisconsin), with whom she has jointly taught landscape ecology courses over the past decade; co-teaching has been inspiring, fun, and has certainly helped shape her thinking.

This book benefited tremendously from valuable critical comments provided by numerous colleagues. We especially thank David Mladenoff and Sarah Gergel, who both read nearly the entire manuscript and provided constructive criticism that has been enormously helpful. David Mladenoff actually read the whole manuscript twice, and Turner especially thanks him for being such a good colleague. In addition, we are grateful to the following friends and colleagues for reviewing one or more chapters: Jeff Cardille, Steve Carpenter, F. S. (Terry) Chapin, Mark Dixon, Tony Ives, Dan Kashian, Jim Miller, Bill Romme, Tania Schoennagel, Steve Seagle, Emily Stanley, Dan Tinker, Phil Townsend, and Kim With. Comments on draft chapters from the students in "Principles of Landscape Ecology," taught at the University of Wisconsin-Madison during the spring 1999 semester, were also very helpful.

The graphics and illustrations for this book were prepared by Michael Turner, and we are indebted to him for greatly improving the visual communication of the concepts and examples in this book. We are delighted with the clarity and consistency of the figures throughout the text. We thank Kandis Elliot (University of Wisconsin) and Michael Mac (Biological Resources Division, U.S. Geological

Survey) for sharing visual resources. Sandi Gardner and Sally Tinker provided valuable editorial assistance in the final stages of manuscript preparation. Finally, we thank the two editors with whom we worked at Springer-Verlag, initially Rob Garber and then Robin Smith, for their patience and support of this effort, especially given the time it has taken us to complete it.

MONICA G. TURNER
Madison, WI

ROBERT H. GARDNER
Frostburg, MD

ROBERT V. O'NEILL
Oak Ridge, TN

January, 2000

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CHAPTER 1 ~ INTRODUCTION TO LANDSCAPE ECOLOGY AND SCALE 1

CHAPTER 1

INTRODUCTION TO LANDSCAPE ECOLOGY AND SCALE

Landscape ecology focuses on the relationships between spatial pattern and ecological processes. From its emergence as a coherent area of research and application in the 1980s, the concepts, theory, and methods of landscape ecology have matured. Its central themes have been widely embraced and assimilated in many branches of ecology. Some authors (e.g., Wiens 2002) have even suggested that landscape ecology catalyzed a paradigm shift in ecology. Whether or not such a shift occurred (sensu Kuhn 1996) has been a great topic for spirited discussion, but there is no doubt that landscape ecology has influenced the way scientists and managers think about the environment. Interest in landscape studies remains fueled by many factors, especially the critical need to understand the rapid, broad scale, and profound changes that are happening all around us.

Most of us have an intuitive sense of the term “landscape”; we think of the expanse of land and water that we observe from a prominent point, and distinguish between agricultural and urban landscapes, lowland and mountainous landscapes, natural and developed landscapes. Any of us could list components of these landscapes—for example, farms, fields, forests, wetlands, and the like. If we have considered how organisms other than humans may see “their” landscape, our own sense of landscape may be broadened to encompass components relevant to a

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honeybee, beetle, vole, or bison. In all cases, our intuitive sense includes a variety of different elements that comprise the landscape, change through time, and influence ecological dynamics. In his 1983 editorial in *BioScience*, Richard T. T. Forman used tangible examples to bring these ideas to the attention of ecologists:

> What do the following have in common? Dust-bowl sediments from the western plains bury eastern prairies, introduced species run rampant through native ecosystems, habitat destruction upriver causes widespread flooding down river, and acid rain originating from distant emissions wipes out Canadian fish. Or closer to home: a forest showers an adjacent pasture with seed, fire from a fire-prone ecosystem sweeps through a residential area, wetland drainage decimates nearby wildlife populations, and heat from a surrounding desert desiccates an oasis. In each case, two or more ecosystems are linked and interacting. (Forman 1983)

In this chapter, we define landscape ecology, briefly review its intellectual roots, introduce key concepts related to scale, and present an overview of the remainder of the book. In addition, some commonly used terms in landscape ecology are defined in Table 1.1.

WHAT IS LANDSCAPE ECOLOGY?

Landscape ecology emphasizes the interaction between spatial pattern and ecological process—that is, the causes and consequences of spatial heterogeneity across a range of scales. The term "landscape ecology" was introduced by the German biogeographer Carl Troll (1939), arising from the European traditions of regional geography and vegetation science and motivated particularly by the novel perspective offered by aerial photography. Landscape ecology essentially combined the spatial approach of the geographer with the functional approach of the ecologist (Naveh and Lieberman 1984; Forman and Godron 1986). During the past three decades, the focus of landscape ecology has been defined in various ways:

> Landscape ecology … focuses on (1) the spatial relationships among landscape elements, or ecosystems, (2) the flows of energy, mineral nutrients, and species among the elements, and (3) the ecological dynamics of the landscape mosaic through time. (Forman 1983)
>
> Landscape ecology focuses explicitly upon spatial patterns. Specifically, landscape ecology considers the development and dynamics of spatial heterogeneity, spatial and temporal interactions and exchanges across heterogeneous landscape, influences of spatial heterogeneity on biotic and abiotic processes, and management of spatial heterogeneity. (Risser et al. 1984)

TABLE 1.1.
DEFINITION OF COMMONLY USED TERMS IN LANDSCAPE ECOLOGY (ADAPTED AND EXPANDED FROM FORMAN 1995).

Term	Definition
Composition	What and how much is present of each habitat or cover type
Configuration	A specific arrangement of spatial elements; often used synonymously with spatial structure or patch structure
Connectivity	The spatial continuity of a habitat or cover type across a landscape
Corridor	A relatively narrow strip of a particular type that differs from the areas adjacent on both sides
Cover type	Category within a classification scheme defined by the user that distinguishes among the different habitats, ecosystems, or vegetation types on a landscape
Edge	The portion of an ecosystem or cover type near its perimeter, and within which environmental conditions may differ from interior locations in the ecosystem; also used as a measure of the length of adjacency between cover types on a landscape
Fragmentation	The breaking up of a habitat or cover type into smaller, disconnected parcels; often associated with, but not equivalent to, habitat loss
Heterogeneity	The quality or state of consisting of dissimilar elements, as with mixed habitats or cover types occurring on a landscape; opposite of homogeneity, in which elements are the same
Landscape	An area that is spatially heterogeneous in at least one factor of interest
Matrix	The background cover type(s) in a landscape, characterized by extensive cover and high connectivity; not all landscapes have a definable matrix
Patch	A surface area that differs from its surroundings in nature or appearance
Scale	Spatial or temporal dimension of an object or process, characterized by both grain and extent

> Landscape ecology is motivated by a need to understand the development and dynamics of pattern in ecological phenomena, the role of disturbance in ecosystems, and characteristic spatial and temporal scales of ecological events.—(Urban et al. 1987)
>
> Landscape ecology emphasizes broad spatial scales and the ecological effects of the spatial patterning of ecosystems.—(Turner 1989)

> Landscape ecology deals with the effects of the spatial configuration of mosaics on a wide variety of ecological phenomena. (Wiens et al. 1993)
>
> Landscape ecology is the study of the reciprocal effects of spatial pattern on ecological processes; it promotes the development of models and theories of spatial relationships, the collection of new types of data on spatial pattern and dynamics, and the examination of spatial scales rarely addressed in ecology. (Pickett and Cadenasso 1995)

Collectively, this set of definitions clearly emphasizes two important aspects of landscape ecology that distinguish it from other subdisciplines within ecology. First, *landscape ecology explicitly addresses the importance of spatial configuration for ecological processes*. Not only is landscape ecology concerned with how much there is of a particular component, it also considers how it is arranged. The underlying premise of landscape ecology is that the explicit composition and spatial form of a landscape mosaic affect ecological systems in ways that would be different if the mosaic composition or arrangement were different (Wiens 1995). Previously, most ecological understanding had implicitly assumed an ability to average or extrapolate over spatially homogenous areas. Ecological studies often attempted to achieve a predictive knowledge about a particular type of system, such as a salt marsh or forest stand, without consideration of its size or position in a broader mosaic. Considered in this way, with its emphasis on spatial heterogeneity, landscape ecology is applied across a wide range of scales (Fig. 1.1). Studies might address the response of a beetle to the patch structure of its environment within square meters (e.g., With et al. 1999), the influence of topography and vegetation patterns on ungulate habitat use at multiple scales (e.g., Boyce et al. 2003), or the effects of land-use arrangements on nutrient dynamics in a watershed (e.g., Strayer et al. 2003b).

Second, *landscape ecology often focuses upon spatial extents that are much larger than those traditionally studied in ecology*—often, the "landscape" as seen by a human observer (Fig. 1.2). In this sense, landscape ecology addresses many different kinds of ecological dynamics across large areas such as the Southern Appalachian Mountains, the Mongolian steppe, Yellowstone National Park, the Mediterranean region, or rainforests of Brazil. However, it is important to note that although these areas are typically larger than those used in most community- or ecosystem-level studies, the spatial scales are not absolutes. We deal with issues of scale later in this chapter and throughout this book, but suffice it to say here that landscape ecology does not define, a priori, specific spatial scales that may be universally applied. Rather, the emphasis in landscape ecology is to identify scales that best characterize relationships between spatial heterogeneity and the processes or response variables of interest. These two aspects—explicit treatment of spatial heterogeneity and a focus on broad spatial scales—are not mutually exclusive and encompass much of the breadth of landscape ecology.

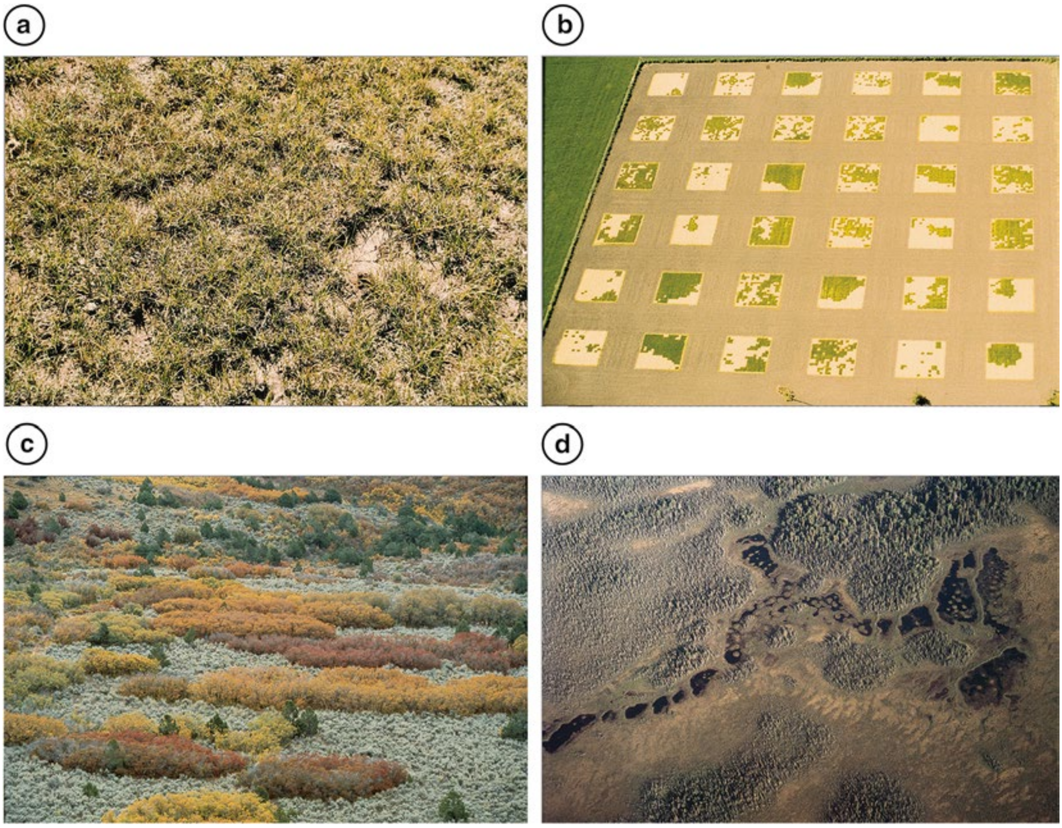

Figure 1.1.

Photos illustrating the concept of landscape as a spatial mosaic at various spatial scales. (**a**) An example of a microlandscape, or landscape complexity from the perspective of a grasshopper. Grass cover is *Bouteloua gracilis* and *Buchloe dactyloides*, and vegetation cover in the ~4 m^2 microlandscape is occasionally disrupted by bare ground. Photo by Kimberly A. With. (**b**) Set of experimental microlandscapes used to explore relative effects of habitat abundance and fragmentation on arthropod communities in an agroecosystem. System consists of a replicated series of 12 plots (each 16 m^2) that vary in habitat abundance and spatial contagion based on fractal neutral landscape models (With et al. 1999). Photo by Kimberly A. With. (**c**) Clones of Gambel oak (*Quercus gambelii*) in Colorado illustrating heterogeneity within approximately 1 km^2. Photo by Sally A. Tinker. (**d**) Aerial view of a muskeg and string bog landscape, Alaska. Photo by John A. Wiens.

The role of humans, obviously a dominant influence on landscape patterns worldwide, is sometimes considered an important component of the definition of landscape ecology. Landscape ecology is sometimes considered to be an interdisciplinary science dealing with the interrelation between human society and its living space—its open and built-up landscapes (Naveh and Lieberman 1984). Indeed, in the landscape ecology approaches characteristic of China, Europe, and the Mediterranean region, human activity is perhaps the central factor in landscape

Figure 1.2.
Photos illustrating different types of landscapes across relatively large areas in the western United States: (**a**) An undeveloped mountainous landscape in the Front Range of Colorado, USA. Photo by Monica G. Turner. (**b**) Landscape mosaic of forest and agricultural land, south of Santiago, Chile. Photo by John A. Wiens. (**c**) Urbanizing landscape outside Denver, Colorado. Photo by John A. Wiens. (**d**) Aerial view of clear-cuts in a coniferous (lodgepole pine, *Pinus contorta*) landscape, Targhee National Forest, Idaho. Postharvest slash piles scheduled for burning can be seen in the clear-cuts. Photo by Dennis H. Knight.

ecological studies (e.g., Fu and Lu 2006; Pedroli et al. 2006). Landscape ecology draws from a variety of disciplines, many of which emphasize social sciences, including geography, landscape architecture, regional planning, economics, and forestry. The role of humans in shaping and responding to landscapes will be considered in many ways throughout this book. For the sake of generality, however, we do not think it necessary to include a human component explicitly in the definition of landscape ecology. Humans clearly create and respond to spatial heterogeneity, and the importance of spatial heterogeneity in linked social–ecological systems is considered throughout this book, along with the importance of landscape ecology for land management and land-use planning.

What, then, is a landscape? We retain a general definition that does not require an absolute scale: *a landscape is an area that is spatially heterogeneous in at least one factor of interest*. Although at the human scale we may observe “a kilometers-wide mosaic over which local ecosystems recur” (Forman 1995), landscape ecology also may deal with “landscapes” that extend over tens of meters rather than kilometers. And despite the “land” in landscape, the concepts of landscape ecology certainly are not restricted to terrestrial settings. Landscapes include aquatic elements and have been defined in freshwater, marine, and benthic systems (e.g., Teixido et al. 2002; Boström et al. 2006; Newton et al. 2008). In addition, one might observe a landscape represented by a gradient across which ecosystems vary but do not necessarily repeat. The above definition is general and flexible, emphasizing the central focus of landscape ecology on the effects of spatial heterogeneity of pattern and process on ecosystem dynamics.

ROOTS OF LANDSCAPE ECOLOGY

Although landscape ecology became more prominent in North America, Australia, and China beginning in the early 1980s, it did not begin de novo at that time but drew upon a rich history established on other continents. The first roots of landscape ecology were in Central and Eastern Europe where biogeographers viewed the landscape through the lens of the human living space, implicitly integrating the environment, the biota, and the human-created components of an area (Naveh and Lieberman 1984). Troll, who coined the term “landscape ecology,” studied biology and then became a geographer. He was impressed by the ecosystem concept as defined by Tansley (1935) and fascinated by the comprehensive view of landscape units depicted on aerial photographs (Zonneveld 1990; Schreiber 1990). He viewed landscape ecology not as a new science, but as a special viewpoint for understanding complex natural phenomena (Schreiber 1990). Rather than taking a narrow view, Troll was remarkably inclusive in his perspective: “…we prefer to speak only of *landscape ecology*, whereby it can remain open whether this includes only the functional interrelations of the natural landscape or also includes the functional connection of human interferences in the cultural landscape” (Troll 1950, translated in Wiens et al. 2007). At about the same time, the Russian scientist Sukachef (1944, 1945) developed the very similar concept of a biogeocoenology, and the British ecologist Watt (1947) laid the foundation of spatial ecology within vegetation science. We strongly urge readers to consult FOUNDATION PAPERS IN LANDSCAPE ECOLOGYy (Wiens et al. 2007), which compiled many of the key primary papers that influenced the early development of landscape ecology in one volume. It is important to understand the foundations upon which any field has been built, and the Wiens et al. edited book provides explanations and commentary along with reproductions of the original papers.

Landscape ecology gained wider acceptance and appreciation in the German-speaking countries of Europe throughout the 1950s and 1960s, and it became closely linked with land planning and landscape architecture (Schreiber 1990; Ruzicka and Miklos 1990; Haber 1990; Zonneveld 1995). There was a strong emphasis on land evaluation, classification, and mapping as the basis from which land-use recommendations could be developed. A Society of Landscape Ecology was founded in The Netherlands in 1972; its members included a wide variety of scientists and practitioners whose concerns ranged from conservation to planning (Zonneveld 1982, 1995). The major literature of landscape ecology from its inception until the early 1980s was predominantly in German and Dutch.

Despite the development of landscape ecology in Europe, the term was virtually absent from North American literature in the mid-1970s (Naveh and Lieberman 1984). A handful of scientists from North America began attending European symposia and workshops on landscape ecology in the early 1980s (Forman 1990) and disseminating these new ideas. Several influential publications in the early 1980s helped to introduce the developing field of landscape ecology to English-speaking scientists. Forman and Godron's (1981) article in *BioScience* asked whether the landscape was a recognizable and useful unit in ecology and provided a set of terms, such as patch, corridor, and matrix, which remain within the common parlance of landscape ecology. Naveh, an ecologist who focused on vegetation science, fire ecology, and landscape restoration, largely in Mediterranean climates, published a review that laid out a conceptual basis for landscape ecology (Naveh 1982); his writing emphasized the integral relationship between humans and the landscape and the importance of a systems approach. These ideas were developed further as a book (Naveh and Lieberman 1984) that delved into both concepts and applications of landscape ecology, and stimulated much discussion among ecologists. Forman's (1983) editorial in *BioScience*, from which we quoted earlier, identified landscape ecology as the candidate idea for the decade, with a richness of empirical study, emergent theory, and applications lying ahead. And although not part of the infusion of ideas from Europe to North America, Romme's study of fire history in Yellowstone National Park, USA (Romme 1982; Romme and Knight 1982) offered a breakthrough in the development of new metrics to quantify changes in the landscape through time.

Two pivotal meetings in the early 1980s helped define the scope of contemporary landscape ecology. A 1983 workshop held at Allerton Park, Illinois, brought together a group of North American ecologists to explore the ideas and potential of landscape ecology concepts (Risser et al. 1984). This meeting came soon after an influential meeting in The Netherlands that drew together landscape ecologists in Europe (Tjallingii and de Veer 1982), and it represented the coalescence of several independent lines of research in the United States. The report that emerged from the workshop (Risser et al. 1984) and subsequent reflections about its influence (Risser 1995; Wiens 2008) still make for good reading. Furthermore, themes discussed at that meeting included topics (e.g., heterogeneity, scale, dynamics, management) that still remain current (Table 1.2). In many respects, a focused search for principles governing the interaction of pattern and process at the landscape scale began at these two meetings. The emphasis of landscape ecology in North America has been somewhat different from Europe, where the association with land planning is so much closer and the landscape more intensively managed. However, landscape ecology still acknowledges its intellectual roots that extend back many decades (Wiens et al. 2007) with questions that continue to revolve around the effects of spatial patterns on ecosystem processes (Wiens 1995). Next we highlight several of the important precursors to the concepts of landscape ecology because of the importance of appreciating the roots of the discipline.

Table 1.2.
Research foci in landscape ecology have changed over time, but commonalities remain in the focus on the causes and consequences of spatial heterogeneity.

Reference	Areas of research emphasis
Risser et al. (1984)	Relationship of landscape heterogeneity to fluxes of organisms, material, and energy
	Historical and present processes that form landscape pattern
	Effect of landscape heterogeneity on spread of disturbance
	Role of landscape ecology in natural resource management
Wu and Hobbs (2002)	Ecological flows in landscape mosaics
	Causes, processes, and consequences of land-use and land-cover change
	Nonlinear dynamics and landscape complexity
	Scaling
	Methodological advances
	Relating landscape metrics to ecological processes
	Integrating humans and their activities into landscape ecology
	Optimization of landscape pattern
	Landscape conservation and sustainability
	Data acquisition and accuracy assessment
Turner (2005)	Interactions: among multiple drivers, especially biophysical and socioeconomic; disturbances; scales; trophic levels
	Spatial nonlinearities, thresholds, and spatial extrapolation
	Ecosystem processes in heterogeneous landscapes
	Expanding the temporal horizons

Intellectual Foundations of Landscape Ecology

Phytosociology and Biogeography

Phytosociologists in Europe and the United States had long studied the spatial distribution of major plant associations (Braun-Blanquet 1932), even going back to the observations of von Humbold (1807) and Warming (1925). For example, it was well known that vegetation distributions in space responded to the north-south gradient of temperature combined with an east-west gradient of moisture. Vegetation pattern was further determined by topographic gradients in moisture, temperature, soils, and exposure. Thus, at broad scales, it was well established that ecological systems interacted with spatially distributed environmental factors to form distinct patterns.

Gradient analysis, an approach similar to the European phytosociology methods, developed in the US as a means for explaining vegetation patterns; Robert Whittaker's analysis of communities in the Great Smoky Mountains (southeastern USA) provides an excellent example (e.g., Whittaker 1952, 1956). In these mountains, distinct vegetation patterns have formed with elevation, due to temperature, and with exposure, due to moisture. In a classic analysis, Whittaker was able to decipher the environmental signals creating the pattern. The complex vegetation system was arrayed on a vertical axis of elevation and a horizontal axis representing exposure from moist sites (mesic) to dry, exposed sites (xeric) (Fig. 1.3). This simple two-dimensional diagram permits one to predict the vegetation type at any spatial location on the landscape based upon its elevation and exposure; such relationships remain quite useful (e.g., Bolstad et al. 1998). Although methods for predicting species distributions are now very sophisticated (e.g., Guisan and Zimmerman 2000; Guisan and Thuiller 2005), the influence of environmental gradients is usually incorporated. Interest in how species and communities may shift with continued global warming has renewed interest in developing and evaluating such approaches.

One line of theory was particularly influential in the development of landscape ecology: island biogeography, the analogy between patches of natural vegetation and oceanic islands. The British biogeographer Lack (1942) had early observed that smaller and more remote offshore islands had fewer bird species. From this, and similar observations, MacArthur and Wilson (1963, 1967) developed a general theory of island biogeography. The theory has two basic parts: (1) the probability of a species reaching an island is inversely proportional to the distance between the island and the source (mainland or source patch) and directly proportional to island size, and (2) the probability of extinction of a species on the invaded island is a function of island size. John Curtis, a Wisconsin plant ecologist, documented human modification of landscapes in the upper Midwest, USA, that produced "islands" of remnant forest and grassland in a "sea" of agriculture (Curtis 1956). Efforts in landscape biogeography that assessed population and community

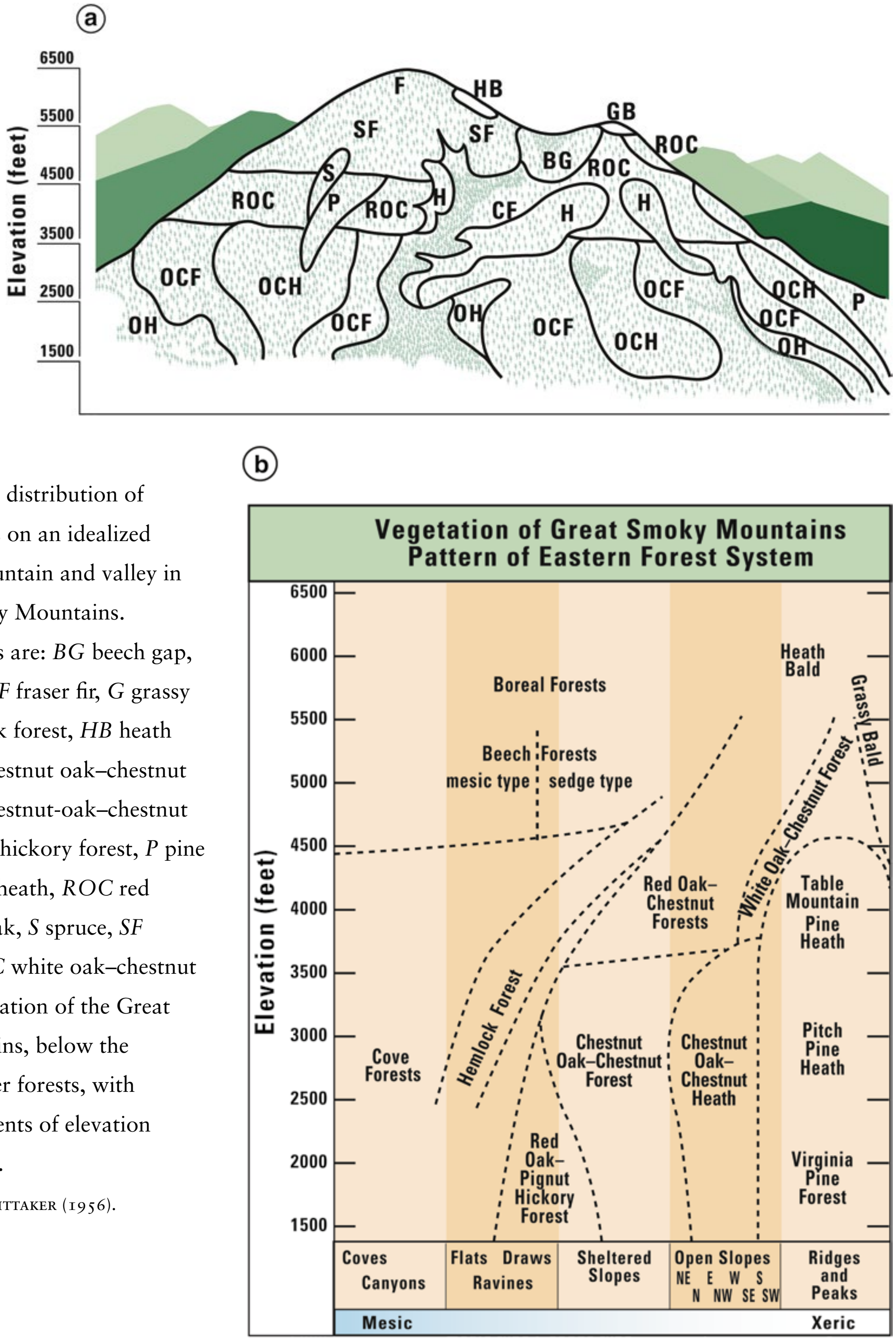

FIGURE 1.3.
(**a**) Topographic distribution of vegetation types on an idealized west-facing mountain and valley in the Great Smoky Mountains. Vegetation types are: *BG* beech gap, *CF* cove forest, *F* fraser fir, *G* grassy balk, *H* hemlock forest, *HB* heath baldm, *OCF* chestnut oak–chestnut forest, *OCH* chestnut-oak–chestnut heath, *OH* oak-hickory forest, *P* pine forest and pine heath, *ROC* red oak–chestnut oak, *S* spruce, *SF* spruce-fir, *WOC* white oak–chestnut forest. (**b**) Vegetation of the Great Smoky Mountains, below the subalpine conifer forests, with respect to gradients of elevation and topography.

ADAPTED FROM WHITTAKER (1956).

responses to fragmented landscapes owe much to this body of theory, although metapopulation models (Hanski 1998) have largely replaced island biogeography models as the theoretical framework within which issues of habitat fragmentation are considered (Baguette and Mennechez 2004). Some authors (e.g., Haila 2002) suggested that island biogeography acted as an "intellectual attractor" that constrained thinking about habitat fragments. As the ideas were increasingly applied to terrestrial habitat fragments, it became apparent that features not considered within island biogeography could be as or more important than fragment size and distance from a source population. Thus, contemporary studies of habitat fragmentation often consider changes in community composition and ecosystem properties over time, edge effects as possible drivers of local extinction, connections between habitat fragments, and the quality of the matrix that surrounds habitat fragments (e.g., Laurance 2008; Damschen et al. 2008; Collinge 2009; Thornton et al. 2011).

Spatial Pattern and Theoretical Ecology

A number of early theoretical population studies considered the interaction between spatial patterning and ecological dynamics for terrestrial (Clark et al. 1978, 1979; Johnson et al. 1992) and aquatic (Steele 1974a; Harris 1998) ecosystems. These studies demonstrated that population interactions are sometimes stabilized by the heterogeneous arrangement of ecological resources (e.g., Reddingius and Den Boer 1970; Hastings 1977; Scheffer and Boer 1995; Roff 1974). At the same time, ecological processes alone can generate complex patterns when resource patterns are homogeneous (Dubois 1975; McLaughlin and Roughgarden 1991; Molofsky 1994). The conclusion drawn by Clark (1980) was that management practices that reduce the spatial heterogeneity of resources may threaten the long-term persistence of ecological systems.

Spatial dynamics predicted by population theory were verified by the classic experiments of Huffaker (Huffaker 1958; Huffaker et al. 1963) who studied the interactions of frugivores and predatory mites in experimentally manipulated arrays of oranges. The oranges provided food for the fructivorous mites that, in turn, were consumed by predatory mites. Spatial manipulation of the oranges could shift dynamics between unstable (oranges placed close together allowing predators to locate and eliminate all prey) and stable (oranges formed into patches preventing predators from locating and eliminating all prey). These experiments provided convincing evidence that spatial relationships were essential if population dynamics were to be understood—a central theme of the work of Andrewartha and Birch (1954). Other studies combining theoretical and empirical approaches also demonstrated that population interactions such as competition could produce patchiness in species distributions, even in the presence of a homogenous template (Okubo 1974; Segal and Levin 1976; Yamamura 1976).

Increased interest in spatial effects led to a series of theoretical studies exploring the biotic (Sprugel 1976) and abiotic (Levin and Paine 1974a, b) template that creates pattern. Levin (1976a) provided an excellent summary, identifying three essential factors: (1) local uniqueness of sites on the landscape caused by variations in microhabitat, soils, etc.; (2) phase differences, such that different points on the landscape are at different stages of recovery from localized disturbances; and (3) dispersal effects in which differential movement by organisms across landscapes leads to patchiness (e.g., Criminale and Winter 1974).

The interplay between spatial heterogeneity with species-specific patterns of dispersal was extensively studied (e.g., Levins 1970; Bradford and Philip 1970; Levins and Culver 1971; Kareiva 1990) and laid the foundation for numerous studies that assessed the effect of landscape heterogeneity on organism movement. Because the spatial pattern of resources provides refuges (Comins and Blatt 1974) that permit individuals to escape unfavorable conditions, the degree to which heterogeneity stabilizes relationships will depend on the relative dispersal ability of predator and prey (Vandermeer 1973; Taylor 1990) and differences in their reproductive rates (Hilborn 1975). The ability to disperse over a gradually changing environment can allow a population to survive extreme conditions (Roff 1974; Hamilton and May 1977). The conclusion from these studies seems clear: spatial pattern can affect both the stability (Jones 1975) and size of populations (Steele 1974b) with population dispersal enhancing persistence by spreading resource utilization over space and time (Myers 1976).

Geographic Sciences

The relevance for landscape ecology of concepts developed in geography has always been apparent (e.g., Meentemeyer and Box 1987). The geographic sciences also made rapid developments in landscape ecology possible through the geographic information sciences (i.e., GIScience) and the methods for management and analysis of spatial data. Although technology does not drive science, advances in geographic information systems (GIS) and remote sensing certainly opened new doors of inquiry. We now have the ability to observe, quantify, and efficiently answer questions about spatial patterns over large areas. Satellite imagery, which first became available (though expensive) in the late 1970s, is now relatively inexpensive and widely available. Although Newton et al. (2009) suggested that landscape ecologists were relatively slow to recognize the full potential of the rapidly evolving remote sensing technologies, the analysis of remote imagery has become an essential element in many landscape studies. Software developments (e.g., GIS and image analysis programs, spatial statistics, etc.) now provide the means to display, superimpose, and analyze spatial patterns. These analytical tools, and the geographer's experience in handling large spatial databases, collectively have been a stimulus and a critical resource for landscape ecologists.

Landscape Planning, Design, and Management

The relationship between human societies and landscape change has been a fundamental concern of ecologists in Europe since the inception of landscape ecology (see Naveh 1982). Indeed, the history of human-induced change is clearly apparent throughout Europe, with roads and viaducts constructed during the Roman Empire still visible in many areas. The initial emphasis of landscape ecological studies in North American was on relatively undisturbed systems (Risser et al. 1984), even though the effects of humans on landscapes have been evident for more than 140 years (Marsh 1864 as cited by Turner and Meyer 1993). The accelerating rate and consequences of landscape change are prompting greater similarity in the North American and European perspectives. A number of authors anticipated the need to integrate ecological studies with landscape planning, developing methods of map overlay (a precursor to current GIS methods) (McHarg 1969); an overview of the effects of ecosystem fragmentation in human-dominated landscapes edited by Burgess and Sharpe (1981); and the development of concepts of adaptive management by Holling (1978).

The goals of landscape planning, design, and management include the identification and protection of ecological resources and control of their use through plans that ensure the sustainability of these resources (Fabos 1985). Consequently, landscape planning is a primary basis for collaboration and knowledge exchange between planners and landscape ecologists (Ahern 1999; Opdam et al. 2001; Nassauer and Corry 2004). Some of the best early examples of the integration of landscape planning, design, and management were found in The Netherlands, where a national plan for a sustainable landscape was implemented (Vos and Opdam 1993). Designing extensive ecological networks for conserving different taxa has also been an important component of land planning across Europe (e.g., Bruinderink et al. 2003). In North America, early examples included plans for ecosystem management of crown forests in Ontario, Canada (Perera et al. 2006) and studies aimed at conservation design (Ando et al., 1998; Diamond and May 1976; Mladenoff et al. 1994). Managing landscapes to meet conservation goals will continue to be necessary (Cumming 2007; Lindenmayer et al. 2008) if ecological resources are to be preserved. Land-change science, which seeks to understand the processes of land-use/land-cover change to inform sustainability science (Turner and Robbins 2008), provides another area of research and application that shares much common ground with landscape ecology and aligns with many issues of land planning and management.

Landscape Ecology Matures

When landscape ecology emerged as a coherent science in the mid-1980s, ideas about the ecological importance of spatial heterogeneity and the importance of studying ecological patterns and processes over large regions were far ahead of empirical studies. This remained true for many years because remotely sensed data were initially scarce, expensive, and difficult to manipulate; spatial data in digital form were not readily available; computing capacity was much more limiting; and attitudes within scientific and resource management communities about these "newfangled" ideas were skeptical (and sometimes even hostile). Now, three decades later, the "landscape" of landscape ecology is vastly different, even as the causes and consequences of spatial heterogeneity remain at the heart of the discipline (Table 1.2). The journal *Landscape Ecology* has been publishing since 1987; publications related to landscape ecology continue to increase and include syntheses (e.g., Fortin and Agrawal 2005); and in 2010, the US chapter of the International Association for Landscape Ecology hosted its 25th annual landscape ecology symposium. There is a well-developed body of concepts, sophisticated analysis methods and spatial models, numerous empirical studies, and a widespread recognition that spatial pattern matters. The ideas and approaches of landscape ecology have been widely assimilated within ecology and environmental science, writ large. Experimental studies have even been conducted at broad scales (e.g., Lindenmayer 2009). The remainder of this book provides a synthesis of the state of the science, but we first introduce terminology and key concepts associated with scale in landscape ecology to set the stage for subsequent chapters.

SCALE AND HETEROGENEITY

Understanding the issues associated with scale is essential in landscape ecology. The importance of scale became widely recognized in ecology only in the 1980s, despite a long history of attention to the effect of quadrat size on measurements and recognition of species/area relationships (Pielou 1969; Arrhenius 1921). The development and spirited discussions of conceptual frameworks that defined the issues of scale (Allen and Starr 1982; Delcourt et al. 1983; O'Neill et al. 1986; Allen and Hoekstra 1992) stimulated ecologists to reconsider how patterns and processes can change with space and time. It quickly became clear that no single set of dimensions in time and space were appropriate for the study of all ecological problems: Some problems required a focus on an individual organism and its physiological response to local conditions (Schreiber and Lloyd-Smith 2009), while other problems required a broad spatial scope to study how species distributions change with time (Guisan and Thuiller 2005). As landscape ecologists began to manipulate spatial data, conduct studies over a spectrum of scales, and develop spatial models, the profound effects of scale on landscape pattern and process simply could not be ignored.

Nearly all ecologists now recognize that "scale" is a critical concept in the physical and natural sciences. In his MacArthur Award Address to the Ecological Society of America, Simon Levin noted "the problem of relating phenomena across scales is the central problem in biology and in all of science" (Levin 1992). Elsewhere in his address, Levin (1992) stated

> …we must find ways to quantify patterns of variability in space and time, to understand how patterns change with scale, and to understand the causes and consequences of pattern. This is a daunting task that must involve remote sensing, spatial statistics, and other methods to quantify pattern at broad scales; theoretical work to suggest mechanisms and explore relationships; and experimental work, carried out both at fine scales and through whole system manipulations, to test hypotheses.

As ecologists began addressing broad-scale questions, they also began to see the implications of selecting scales for research. Researchers became aware that the overall extent of the area studied would affect the numerical result or pattern obtained, and seemingly disparate results from different studies might be due to differences in the scales at which they were conducted. While understanding change in pattern with scale had strong historical roots (Greg-Smith 1952), the expanded application of the scale concept in the design and interpretation of surveys, comparative studies, and controlled experiments was new (Schneider 1994). Ecologists also realized that scales important to humans were not necessarily relevant for other organisms or ecological processes, and biological interactions occur at multiple scales (Wiens 1989). This increased focus on scale is an enduring change in how ecological research is pursued (Schneider 1998; Wu et al. 2006).

Three important publications laid the foundation for the treatment of scale in ecology. First, Allen and Starr's (1982) book on hierarchy theory laid out novel ways of considering scale that emerged from general systems theory and instigated tremendous discussion in all branches of ecology. Second, the Delcourt et al. (1983) article on scales of vegetation dynamics in space and time synthesized paleoecological changes in landscapes and graphically presented the positive correlation of spatial and temporal scales as a time–space state space that has been widely used (Fig. 1.4). Third, the book by O'Neill et al. (1986) reviewed the concept of an ecosystem, then proposed a hierarchical framework for ecosystems. In addition to these ecological studies, the new mathematical theory of fractals (Mandelbrot 1983) provided insights into the complicated patterns often seen in nature and offered novel approaches to extrapolate observations from one scale to another. Collectively, these events and insights engendered an appreciation for concepts of scale and a mandate to better understand its effects in ecology.

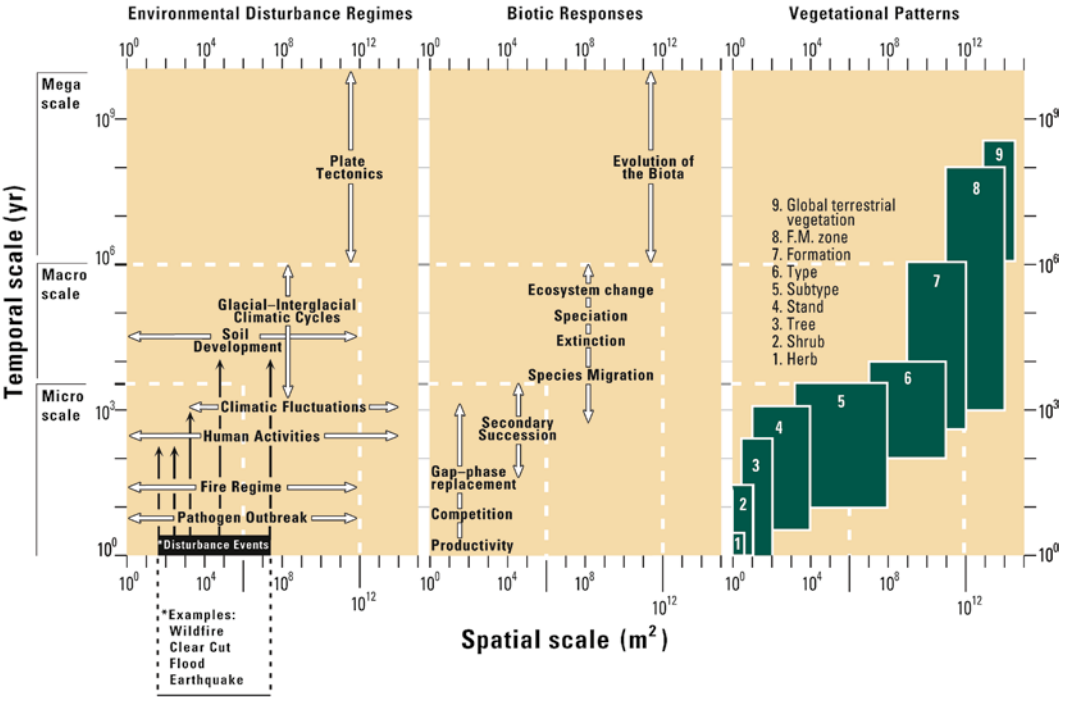

FIGURE 1.4.

Space–time hierarchy diagram proposed by Delcourt et al. (1983). Environmental disturbance regimes, biotic responses, and vegetational patterns are depicted in the context of space–time domains in which the scale for each process or pattern reflects the sampling intervals required to observe it. The time scale for the vegetation patterns is the time interval required to record their dynamics.

MODIFIED FROM DELCOURT ET AL. (1983).

Scale Terminology

Landscape ecologists must be unambiguous in their use of scale-related terms. *Scale* refers to the spatial or temporal dimension of an object or a process (Table 1.3). This is distinguished from *level of organization*, which is used to identify a place within a biotic hierarchy (Table 1.3). For example, a sequence of differing levels of organization might be: organism, deme, population, community, and biome. Each level of organization is characterized by a variety of processes that have their own scales of space and time. A population of a particular species may occupy a given amount of space, move or disperse a set distance, and reproduce within characteristic time period. However, the community to which that population belongs is characterized by the spatial and temporal scales of all populations within the community.

Scale is characterized by grain and extent (Fig. 1.5). *Grain* refers to the finest spatial resolution within a given data set; for example, grain refers to the cell size for gridded maps or the minimum mapping unit of maps drawn with polygons. *Extent* refers to the size of the overall study area. Grain and extent are easy to think

Table 1.3.
Definitions of scale-related terminology and concepts

Term	Definition
Scale	Spatial or temporal dimension of an object of process, characterized by both grain and extent
Level of organization	The place within a biotic hierarchy (e.g., organism, deme, population)
Cartographic scale	The degree of spatial reduction indicating the length used to represent a larger unit of measure; ratio of distance on the map to distance on the earth surface represented by the map, usually expressed in terms such as 1:10,000. In cartography, large scale = fine resolution, and small scale = coarse resolution
Resolution	Precision of measurement; grain size, if spatial
Grain	The finest level of spatial resolution possible within a given data set
Extent	The size of the study area or the duration of time under consideration
Extrapolate	To infer from known values; to estimate a value from conditions of the argument not used in the process of estimation; to transform information (a) from one scale to another (either grain size or extent) or (b) from one system (or data set) to another system at the same scale
Critical threshold	Point at which there is an abrupt change in a quality, property, or phenomenon
Absolute scale	The actual distance, direction, shape, and geometry
Relative scale	A transformation of absolute scale to a scale that describes the relative distance, direction, or geometry based on some functional relationship
Hierarchy	System of interconnections or organization wherein the higher levels constrain and control the lower levels to various degrees depending on time constraints of the behavior
Holon	Representation of an entity as a two-way window through which the environment influences the parts, and parts communicate as a unit to the rest of the universe (Koestler 1967)

of when considering remote imagery. Different satellite sensors have different cell sizes or grain; for example, there is a 10-m by 10-m cell size for SPOT panchromatic imagery, 30-m by 30-m for Landsat Thematic Mapper imagery, 90-m by 90-m for the earlier Landsat Multispectral Scanner imagery, and 250-m by 250-m for MODIS. The detail that can be gleaned from these different sensors varies, in part, because of the differences in grain. Extent can vary independently of grain,

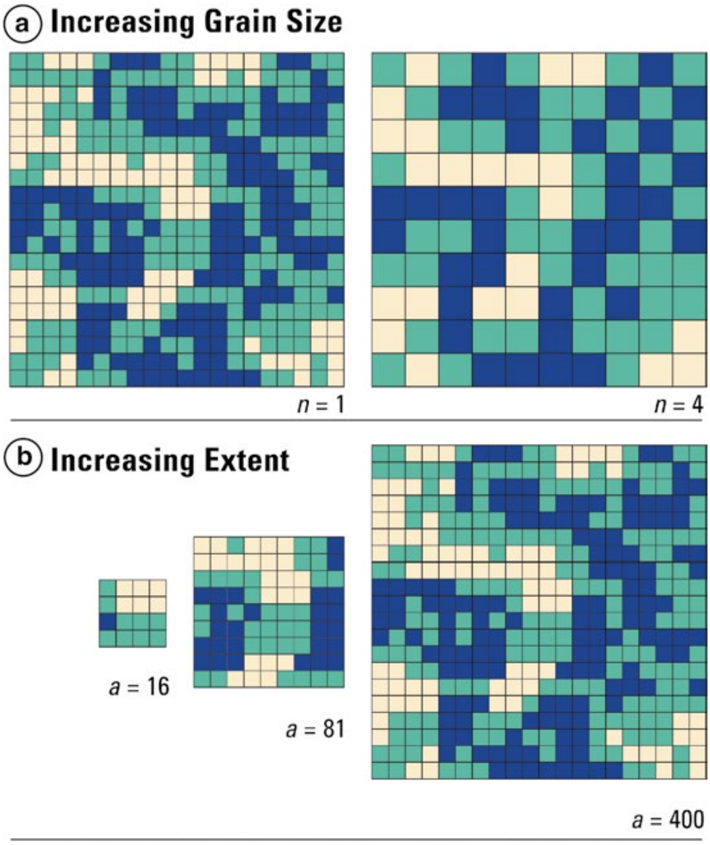

FIGURE 1.5.
Schematic illustration of two components of spatial scale, (**a**) grain and (**b**) extent. The number of cells aggregated to form the new data unit (i.e., new grain size) is indicated by *n*; total area, or extent, is indicated by *a*.
MODIFIED FROM TURNER ET AL. (1989B).

although there is some degree of correlation; for example, a small extent usually requires a small grain size. When we say that a pattern, process, or phenomenon is *scale dependent*, we mean that it changes with the grain or the extent of the measurement. Schneider (1994) defines scale-dependent processes as those in which the ratio of one rate to another varies with either resolution (grain) or range (extent) of measurement.

One source of confusion is that ecologists and geographers often mean the opposite when they say "large" or "small" scale. The long-standing use in geography of *cartographic scale* refers to the degree of spatial reduction indicating the length used to represent a larger unit of measure (Table 1.3). Cartographic scale is typically expressed as the ratio or representative fraction of distance on the map to distance on the surface of the earth that is represented on a map or aerial photograph, e.g., 1:10,000 or 1:100,000. When geographers and cartographers say "large scale," they mean very fine resolution (e.g., 1:500), which in practice means a very large map of a small spatial extent; similarly, when they say "small scale," they mean very coarse resolution, or maps of large areas that do not contain much detail (e.g., 1:250,000). This use of small and large is opposite to what ecologists usually mean by those terms! To avoid confusion, we recommend and use here the terms "fine" and "broad" to modify scale, such that fine scale refers to small areas, greater resolution, and more detail, and broad scale refers to larger areas, lower resolution, and less detail. In practical terms, the scale at which you make any measurement—e.g., the size of the quadrat, length of transect, area of census, size of the grid cell in remotely sensed data—influences the numerical answer obtained and must be defined explicitly.

When we seek to *extrapolate* (Table 1.3), we attempt to infer from known values, that is, to estimate a value from conditions beyond the range of the data used in the process of estimation (Miller et al. 2004). For example, we extrapolate when we use a regression line to predict values of y based on a value of x that is beyond our original data. We also extrapolate when we transfer information from one scale to another (either grain size or extent), often called "upscaling" or "downscaling," or from one system (or data set) to another system at the same scale. Upscaling is often done by adding or averaging fine-grained units to estimate a property of a larger area, such as estimating carbon stocks across a landscape by summing individual grid cells. An example of downscaling is translating climate data or projections from the large grid cells used in general circulation models to finer scales by incorporating additional information, such as topography. The search for techniques or algorithms to extrapolate across scales or among landscapes remains an important research topic in landscape ecology. In practical terms, this occurs because scientists never have all the data they need at all the "right" scales. Extrapolating may be straightforward in some cases when the relationship of a variable with changes in scale is linear, or additive; however, if the relationship is nonlinear and/or there are *critical thresholds* at which there is an abrupt change, then extrapolation is problematic. The extrapolation of estimates of species richness with increased size of a study area is a classic example of scale dependency: At fine scales (small areas) species richness increases linearly with area, but as area sampled continues to increase, the relationship will eventually plateau, causing simple linear extrapolations to greatly overestimate species richness for very large areas. Although the exact reason for the asymptotic species-area curve remains uncertain (Huston 1994), we have enough data for many species groups and landscapes to make reliable empirical extrapolations across scale.

Hierarchy Theory and Cross-Scale Interactions

Hierarchy theory is concerned with the ecological consequences of levels of organization in ecological systems (O'Neill et al. 1986) and has been influential in landscape ecology. In the simplest series (cell, organism, population, community), each level is composed of subsystems (e.g., the next lower level for organisms are cells) and is constrained by the level above it (populations constrain organisms). Ecological organizations do indeed show hierarchical structure (Rowe 1961), with emergent properties that affect ecological processes at a variety of scales.

Here, we briefly highlight some of the important take-home messages from hierarchy theory that are especially significant to landscape ecologists.

A *hierarchy* is defined as a system of interconnections wherein the higher levels constrain the lower levels to various degrees, depending on time constraints of the behavior. The concept of hierarchy has a long history in science, but Koestler's (1967) "The ghost in the machine" was a landmark publication. Koestler identified entities that were at the same time composed of parts yet also a whole that fits within its environment. At every level in a hierarchy there are these elements, termed *holons*, that are both wholes and parts.

Within a hierarchical system, the levels are distinguished by differences in the rates, or frequencies, of their characteristic processes (Fig. 1.6). Holons have characteristic rates of behavior, and these rates place them at certain levels in the hierarchy of holons. For example, an individual organism, as a holon, can interact with other individual organisms because both operate at the same space–time scale. But, an individual organism cannot interact with a biome—they are orders of magnitude different in scale. To the individual organism, the biome is a relatively constant background or context within which it operates. Thus, temporal scales serve as important criteria for identifying levels within a hierarchy, and there are different scales of space and time over which controls operate.

An important concept from hierarchy theory is the importance of considering at least three hierarchical levels in any study (Fig. 1.7). The focal level or level of interest is identified as a function of the question or objective of the study. For example,

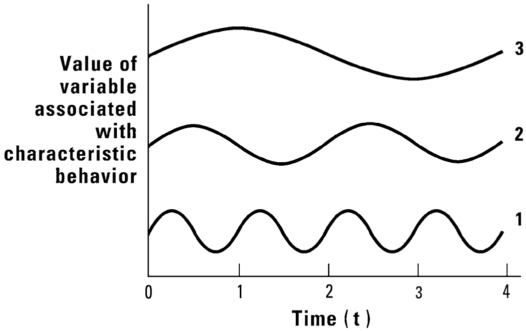

Figure 1.6.

Value of variables associated with a level of an ecological hierarchy as they change through time. The *top line* (*line 3*) is a slow variable, one that would serve as a constraint to the lower levels; this may change so slowly that it is perceived as a constant by an observer. The *middle line* (*line 2*) might be the scale at which an observer measures change in the system. The *lower line* (*line 1*) is a fast variable, one that might change so quickly that it could be perceived as a constant.

Redrawn from Allen and Starr (1982:12).

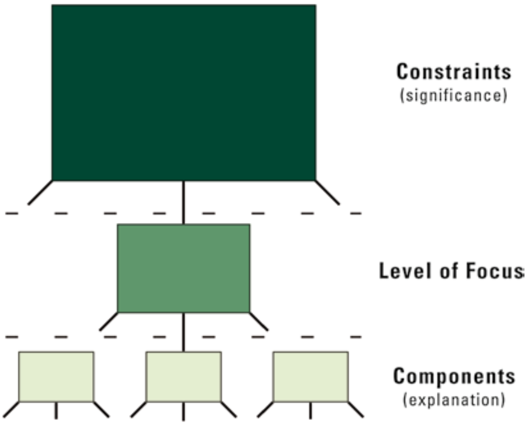

FIGURE 1.7.
Illustration of the three levels in a hierarchy. Upper levels constrain the focal level and provide significance; lower levels provide details required to explain response of focal level.
ADAPTED FROM O'NEILL ET AL. (1986).

answering the question, "What is the effect of insect herbivory on tree growth rate" would require focusing upon individual trees, whereas, "What is the effect of insect herbivory on the distribution of live and dead trees across the landscape?" would require focusing on the forest as a whole. Two additional levels then must be considered. The level above the focal level constrains and controls the lower levels, providing context for the focal level. The level below the focal level provides the details needed to explain the behavior observed at the focal level.

A second important take-home message is that although the variables that influence a process may or may not change with scale, a shift in the relative importance of the variables or the perceived direction of a relationship often occurs when spatial or temporal scales are changed. There are numerous examples of this. For example, predicting the rate of decomposition of plant material at a very local scale requires detailed knowledge of the microclimate, variability in the environment, and characteristics of the litter such as its lignin content; however, effectively predicting rates of decomposition at regional to global scales can be done based solely on temperature and precipitation (Meentemeyer 1984). Studies of oak seedling mortality at local scales in the western US showed that mortality decreased as precipitation increased, whereas studies at regional scales demonstrated the mortality decreased in the drier latitudes (Neilson and Wullstein 1983).

Increasing the time frame of observation of a system may lead to different observations and conclusions about the function of the system (e.g., Sollins et al. 1983; Magnuson 1990). The results of different processes become apparent at different temporal scales (Fig. 1.8), and conclusions about the directional change may change qualitatively as observation time increases. The constraint of having a limited observation window has been characterized as "the invisible present" (Magnuson 1990), and this has been illustrated numerous times with long-term ecological data. This issue continues to play into current discussions of global warming, as inference about directional change in climate depends can vary depending on the decades of observation selected.

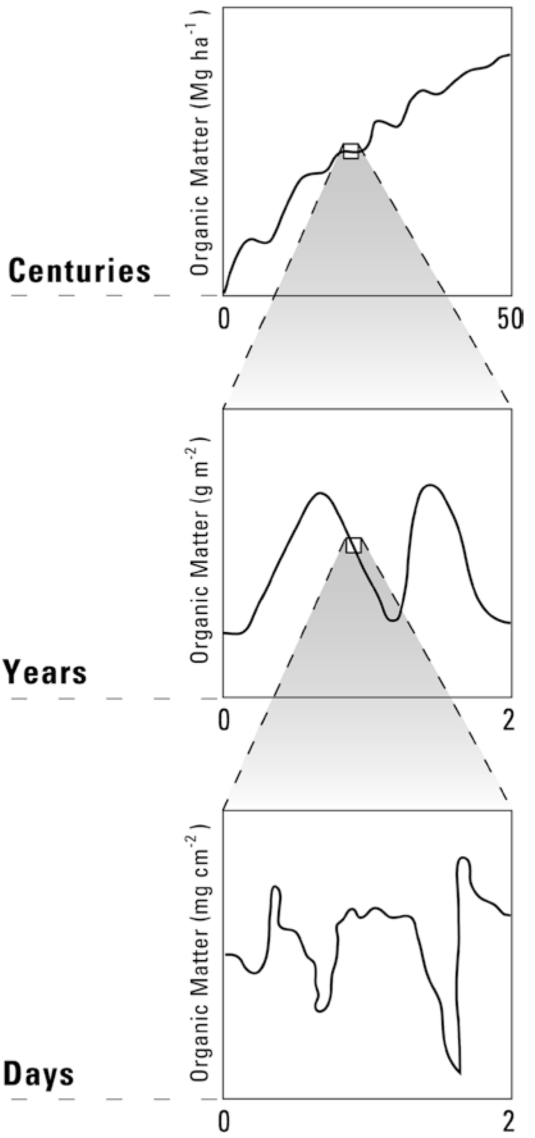

FIGURE 1.8.
Changes in the apparent dynamics of organic matter in the soil when the temporal scale of observation changes. An observation window of days (*lower panel*) reveals rapid fluctuations in litter due to wind and arthropod activity. Over a scale of years (*middle panel*), seasonal patterns of decomposition are apparent. Over a scale of centuries (*upper panel*), the accumulation of organic matter is observed with oscillations that relate to succession.

ADAPTED FROM SOLLINS ET AL. (1983).

Hierarchy theory suggests that multiple scales of pattern will exist in landscapes because of the multiple scales at which processes are acting. Consider the processes that may give rise to pattern in a hypothetical forest landscape. Over broad scales of space and time, geomorphological processes result in distributions of substrate and soil that influence what tree species might occur at what positions. Within the forest that develops, the pattern and frequency of large disturbances such as fire or pathogen epidemics may generate a coarse-grained pattern of different successional stages across the landscape. Local processes of individual tree death may result in small "canopy gaps" distributed throughout the forest landscape. Collectively, then, the spatial pattern of forest communities at any given time in this landscape may reflect these three processes operating over different scales of space and time. An analysis of the spatial pattern of the forest communities across the landscape may well detect these multiple scales of pattern (e.g., Kuuluvainen et al. 1998).

Understanding how or when processes that operating at different scales interact with each other—currently referred to as *cross-scale interactions*—has seen recent renewed interest driven largely by numerous studies showing that spatial pattern affects ecological process (Peters et al. 2004b). Cross-scale interactions are important because they can generate emergent behavior that cannot be predicted based on observations at single or multiple, independent scales, and the interactions may produce nonlinear dynamics with thresholds (Peters et al. 2004b). These ideas build from hierarchy theory but incorporate space, recognize the possibility for a series of cascading thresholds and add two key considerations. First, Peters et al. argue that connectivity among focal units is very important for propagating changes through a system, and that thresholds in connectivity can lead to unexpected and rapid change. Second, the amount and spatial arrangement of focal units can influence the relative importance of the scales that may govern or constrain the dynamics of the system. Such cross-scale interactions and cascading thresholds provide a useful framework for understanding the widespread outbreaks of native bark beetles in western North America (Raffa et al. 2008). In social–ecological systems, the processes that operate at distinct scales, such as individual patches, farms, and entire regions, can interact to produce "cascading thresholds" wherein the crossing of one threshold may induce the crossing of other thresholds and lead to alternative states (Kinzig et al. 2006).

Thus, hierarchy theory tells us that attention should be focused directly on the scales at which phenomena of interest occur; there is no single correct scale for studying landscapes or any other ecological system; and that if we change the scales, the relevant processes or even the direction of relationships that we observe may well change. The scale of interest must be dictated by the question or phenomenon of interest. Finer-scale processes may be viewed as the details required to "explain" the phenomena at the focal scale while broader-scale patterns are the "constraints" that limit the potential range of rate processes. Processes that interact across scales, however, can lead to surprising outcomes. These concepts are rich and provocative, but still leave us with the critical challenge of identifying the proper scale at which to address a given problem.

Returning to Levin's (1992) MacArthur address, we read "That there is no single correct scale or level at which to describe a system does not mean that all scales serve equally well or that there are not scaling laws." Developing the rules for identifying the correct scale for a particular question continues to be an important topic of current research.

Upscaling and Downscaling

The quantitative issues associated with extrapolating to broader scales in space and time—"scaling up"—or to finer scales—"scaling down"—continue to present challenges in landscape ecology (see Wu et al. 2006). Most ecological measurements have been made at relatively fine scales (e.g., square meters or hectares), while predictions of effects are often needed at broad scales (e.g., habitat restoration and conservation, invasive species, disturbance regimes, and climate change).

The simplest approach to scaling across space is to multiply a measurement made at one scale (e.g., unit of area) to predict at a broader scale. For example, a standing biomass for a 10,000-ha forest might be predicted by multiplying the amount of biomass measured in a 1-ha stand by the factor of 10,000. Termed "lumping" by King (1991) and "direct scaling" by Miller et al. (2004), this approach assumes that the properties of the system do not change with scale, and that the broader-scale system behaves like the average value of the finer-scale system—i.e., the system is scale invariant. From a modeling perspective, this assumption holds only if the equations describing the system are linear. Direct scaling can lead to considerable bias because it does not account for additional variability (spatial or temporal) encountered in the scaling process and ignores nonlinear changes in the variable of interest that often occurs with changes in scale (Rastetter et al. 1992). The nature of the bias will depend on the specifics of the spatial dependencies and/or nonlinearities in the system (O'Neill 1979a, b). This approach should only be used with careful consideration of the potential errors and biases that may result.

An improvement upon the simple linear method to scaling is an additive approach that accounts for spatial variability within an area of relatively large extent. *Direct extrapolation* (sometimes referred to as "paint by numbers") uses data or model simulations from a tractable number of discrete elements within a landscape. For example, instead of assuming that biomass is the same throughout the 10,000-ha forest, we recognize that biomass varies with stand age and composition and that we can account for this spatial variability by mapping or using a remote image. In this case, we use empirical measurements to estimate the biomass in each of the types we define, then multiply by the area of each type within the 10,000-ha forested landscape and sum the results (e.g., Burke et al. 1990). This approach is widely used and works reasonably well for quantities such as biomass or net primary production, which themselves do not interact spatially and which can be related to attributes that can be measured remotely over large areas (e.g., color of the ocean, vegetation composition).

A more sophisticated variation on this theme is *extrapolation by expected value* (King 1991), or extending the analogy above, "advanced paint by numbers." This approach recognizes that multiple predictor variables may themselves differ across the landscape and incorporates those into statistical or simulation models.

The general algorithm for this approach entails (1) a model simulating local behavior of a system, (2) a larger landscape over which the model is to be extrapolated, (3) the frequency distributions of variables that describe landscape heterogeneity, and (4) calculation of expected values of the system behavior as a function of the variables describing the heterogeneity of the landscape. The relationship between the predictors and response variable need not be linear, but the values for each predictor must be available for all locations across the landscape. Thus, a principle source of error in this approach lies in the estimation of the probability or frequency distributions of the landscape variables. Like direct extrapolation, the simpler approaches to extrapolation by expected value do not account for spatial interactions or feedbacks, although they can consider the landscape surrounding a focal location and thus represent some broader spatial context.

It is important to note that the error, or variance, associated with the original measurements should also be scaled accordingly to estimate confidence in predictions at the broader scale. There are several excellent examples of mapping a predicted value and also providing a map of uncertainty (Fig. 1.9). However, the general problem remains easier to recognize than to resolve; confidence intervals around a measurement made at one scale may not translate directly to another scale (Schneider 1994). Some quantities increase in variance as scale increases—the so-called pink or red noise identified by spectral analysis (Caswell and Cohen 1995; Cohen et al. 1998; Platt and Denman 1975; Ripley 1978). This may occur when the extent of observations is increased and greater environmental heterogeneity is encountered. For example, the air temperature of a small area might be characterized by a mean temperature, say 11 °C, with a small range of values, say ±1 °C. As extent increases in topographically rough terrain, sites with temperatures ranging from 6° to 24° may be included, resulting in an increase in the variance even if the mean value remains constant. Thus, as the grain becomes coarser the cell characterized by a single temperature may also have greater variability.

Rastetter et al. (1992) and Wiens et al. (1993) suggest that a combination of approaches is needed to scale up, and Miller et al. (2004) provide an overview of methods (Fig. 1.10). The multiplicative approach can be implemented as a first approximation with the recognition that it may work in some cases, but be widely off the mark in others. Additional detail can be added as needed, either through improving the computations at the finer scales (Wiens et al. 1993) to reduce the error that would be translated to the broader scale, or by identifying the spatial subunits across which extrapolations can be summed (Rastetter et al. 1992). From their review of scaling studies, Miller et al. (2004) also note that extrapolations tend to be most reliable when the response variables are closely associated with environmental features that can be mapped accurately. But another point emphasized by Miller et al. bears mention here—the numerous opportunities for learning through the process of scaling. Extrapolations represent spatially explicit predictions that can be tested and used to assess understanding. By examining the

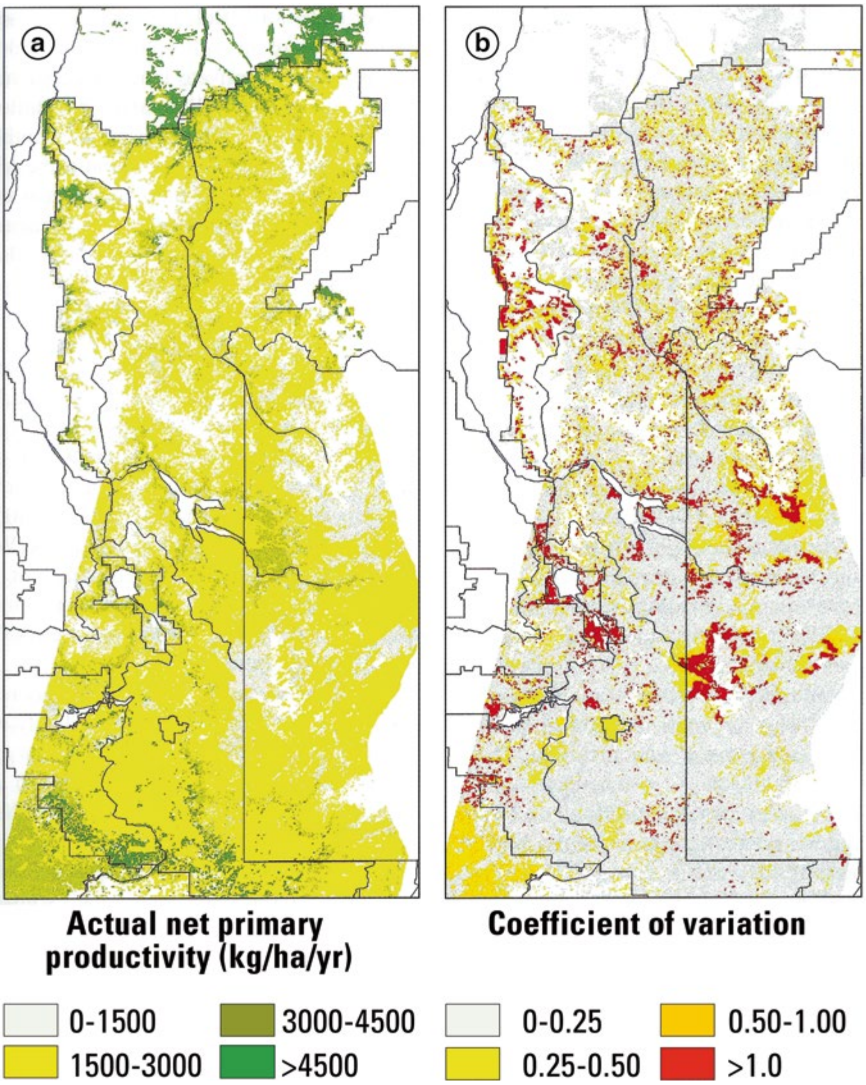

FIGURE 1.9.

Spatial extrapolation of patterns of aboveground net primary production in the western portion of Greater Yellowstone, Wyoming and Montana, USA (**a**) and the map of uncertainty associated with the predictions (**b**).

ADAPTED FROM HANSEN ET AL. (2000).

conditions under which extrapolation fails or succeeds, we can enhance our understanding of the relationships between pattern and process (Miller et al. 2004).

Although our discussion has focused on processes associated with "scaling up"—that is, moving from fine scale measurements to predictions at broad scales—the inverse process of "scaling down" is also an important. For example, the temperature and precipitation patterns predicted by the general circulation models

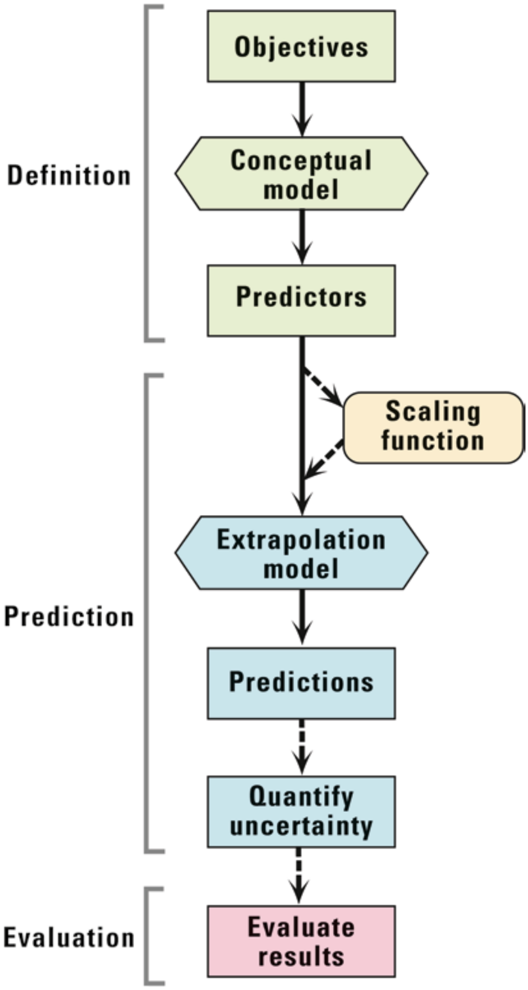

FIGURE 1.10.
A basic framework describing the different components of ecological extrapolation. *Solid arrows* indicate steps that are typically included in the process, whereas *dotted arrows* indicate steps that are not included as commonly but should be.
Adapted from Miller et al. (2004).

used to simulate potential changes in global climate typically have a coarse resolution of 1° or 2° latitude and longitude. However, precipitation and temperature vary considerably within areas that are 100 km × 100 km in size, and this variability is important for local ecological processes (Kennedy 1997; Lynn et al. 1995; Russo and Zack 1997). Using a rather different example, tabulations of population density or housing units for a census tract do not account for the spatial variability within the census tract, yet this variation may be most important for predicting future patterns of land-use change or the movement of nutrients from land to water. Recognition of the importance of developing methods for extrapolating information from coarse to fine grains has increased greatly with the wide use of GIS technologies. Progress in this arena lagged somewhat behind upscaling studies because of the immense data requirements for verifying such extrapolations, but recent developments are encouraging. For example, using data for four national parks in the

USA, Gardner et al. (2008) demonstrate a flexible new method for rescaling (either downscaling or upscaling) land-cover data. Unresolved issues in scaling revolve around the complex responses of ecosystems to change in multiple drivers, the insufficiency of measurements in time and space, and the diversity of approaches being employed across many disciplines. Thus, it is important for landscape ecologists to be informed about the importance of scale and the complexities of scaling, and to continue to make headway in resolving these issues.

OBJECTIVES OF THIS BOOK

Landscape ecology has a rich intellectual history, and it draws upon a wide range of natural and social science. The remainder of this book will deal with the concepts, questions, methods, and applications of landscape ecology with an emphasis on the ecological approach. This in no way diminishes the importance of the social sciences in the interdisciplinary study of landscapes, and we incorporate the human dimension in many ways; however, this text is written by ecologists, and our biases and expertise fall within the science of ecology. We hope that the book will be useful not only to students in ecology but also to students in disciplines such as conservation biology, resource management, landscape architecture, land planning, geography, and regional studies who wish to delve more deeply into landscape ecology as an ecological science. In addition, we hope this volume will complement other landscape ecology books that have different emphases (e.g., Bissonette and Storch 2003; Lovett et al. 2005; Farina 2006; Green et al. 2006; Lindenmayer and Hobbs 2007; Steiner 2008; Collinge 2009; Liu et al. 2011; Tongway and Ludwig 2011).

Landscape ecology may also serve as a source of new ideas for other disciplines within ecology. For example, aquatic ecologists have applied a landscape ecological approach to the study of riffle, cobble, and sandy substrates within streams (e.g., Wohl et al. 1995); patch distributions of fishes as measured by echolocation (e.g., Magnuson et al. 1991; Nero and Magnuson 1992); patterns and processes of rocky benthic communities (e.g., Garrabou et al. 1998); and spatial variation in coral bleaching (Rowan et al. 1997). Thus, landscape ecology benefits from and but also contributes toward the intellectual developments in other disciplines.

This is not a textbook for GIS or remote sensing, although landscape ecology makes extensive use of these technologies. There are many fine texts that are excellent resources for the landscape ecologist who needs a more thorough introduction to these subjects. For GIS, we suggest Thurston et al. (2003), Longley (2005), and Bolstad (2012); for remote sensing, we suggest Campbell (2006) and Jensen (2009).

We have organized the book in a sequence comparable to what we teach in a landscape ecology course. The first section includes two chapters that introduce landscape ecology and scale (Chap. 1) and consider the causes of landscape pattern, including both biotic and abiotic factors, and extended temporal scales (Chap. 2). The next section includes three chapters that cover quantitative approaches in landscape ecology, including landscape models (Chap. 3), landscape metrics (Chap. 4), and spatial statistics (Chap. 5). The next three chapters deal with particular pattern–process relationships that have received considerable attention in landscape studies: disturbance dynamics (Chap. 6), responses of organisms to spatial heterogeneity (Chap. 7), and ecosystem processes at landscape scales (Chap. 8). Finally, we deal explicitly with a myriad of applications of landscape ecology (Chap. 9) and suggest conclusions and future directions for the field (Chap. 10).

SUMMARY

Landscape ecology has come to the forefront of ecology and land management in recent decades, and it is still expanding very rapidly. Landscape ecology emphasizes the interaction between spatial pattern and ecological process—that is, the causes and consequences of spatial heterogeneity across a range of scales. Two important aspects of landscape ecology distinguish it from other subdisciplines within ecology. First, landscape ecology explicitly addresses the importance of spatial configuration for ecological processes. Second, landscape ecology often focuses upon spatial extents that are much larger than those traditionally studied in ecology. These two aspects—explicit treatment of spatial heterogeneity and a focus on broad spatial scales—are complementary and encompass much of the breadth of landscape ecology. Landscape ecology has a history, with its roots in Central and Eastern Europe. The recent search for principles governing the interaction of pattern and process at the landscape scale began with two influential workshops in the early 1980s in Europe and North America.

Scale is a prominent topic in landscape ecology because it influences the conclusions drawn by an observer and whether inferences can be extrapolated to other places, times, or scales. Scale refers to the spatial or temporal dimension of an object or a process, and this is distinct from “level of organization,” which is used to identify a place within a biotic hierarchy. Scale is characterized by grain—the finest level of spatial resolution possible within a given data set, and extent—the size of the overall study area. The related concept of cartographic scale refers to the degree of spatial reduction indicating the length used to represent a larger unit of measure. In practical terms, the scale at which you make any measurement influences the numerical answer obtained. Hierarchy theory is closely related to scale and provides a framework for organizing the complexity of ecological systems.

A hierarchy is defined as a system of interconnections wherein the higher levels constrain and control the lower levels to various degrees, depending on time constraints of the behavior. The levels within a hierarchy are differentiated by their rates of behavior. Ecological studies should consider three levels within a hierarchy: the focal level, the level above, which provides constraint and context, and the level below, which provides mechanism. When scales change, a shift in the relative importance of variables or the perceived direction of a relationship may also change. In addition, understanding how processes operating at different scales in spatially heterogeneous landscapes may interact and produce unexpected changes has emerged as a topic of substantial current interest.

Scale issues often arise in attempting to extrapolate ecological studies to larger or smaller scales. The current understanding has led to a few useful "rules of thumb" for extrapolation. Scale changes may be ignored in homogenous space but not under conditions of spatial heterogeneity. Average dynamics can be applied to a larger area only when the area is homogeneous for the characteristic of interest. If the spatial heterogeneity is present but it is random rather than occurring with a structured pattern, then the average plus the variance can be used to apply local measurements to the broader area. When spatial heterogeneity combines with nonlinear dynamics and the possibility of major changes in constraints, then extrapolation becomes a very difficult problem that does not, at present, have any simple solution. However, substantial progress has been made in upscaling and downscaling data or predictions for specific applications.

There is no "right" scale for landscape ecological studies. Scales must be selected based on the question or objective of a study. However, identifying the appropriate scale remains challenging, and developing methods for doing so remains a topic of current research. Ecologists are still learning how to take the knowledge we have gleaned about patterns and processes at multiple scales into consideration when developing field studies and models, and develop the techniques for extrapolating across scales and landscapes.

DISCUSSION QUESTIONS

1. Consider the two different ways in which ecologists use the concept of landscape—as a relatively large area composed of elements that we recognize, and as a theoretical construct for considering spatial heterogeneity at any scale (see Pickett and Cadenasso 1995). Are these notions mutually exclusive or complementary? Do they confuse or enhance our understanding? Do you think one view is better than the other?
2. Describe three contemporary issues that require consideration of the landscape, either as a driver of change in another variable, or as an element that responds to some driver. What information or understanding is lost if a landscape perspective is not taken?

3. Is landscape ecology defined by its questions or by its techniques? Do you consider it to be a broad or narrow avenue of inquiry within ecology?
4. Select a landscape of your choice and list the important ecological processes that occur in the landscape. Next, estimate the temporal and spatial scales over which these processes operate and plot these in a time–space state space (see Fig. 1.4). How might such a diagram assist you in selecting appropriate scales for a field study or model? What scales are appropriate for different hypotheses you might test?
5. Describe how scale may be considered as both a problem and an opportunity.

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CHAPTER 2

CAUSES OF LANDSCAPE PATTERN

When we view a landscape, we look at its *composition* and *spatial configuration*—that is, what elements are present and in what relative amount, and how these elements are arranged. In an agricultural landscape, we may observe forests occurring along streams and on steep ridges, whereas croplands and pastures occupy upland areas of gentler slope. In a fire-dominated boreal forest landscape, we may see expanses of old forest, young forest, and early successional vegetation. In a deciduous forest, we may observe small gaps in an otherwise continuous canopy of trees, and we may detect boundaries between forests dominated by different species of trees. In landscapes of small extent (e.g., 100 m by 100 m), we may observe complex patterns of vegetated and unvegetated surfaces. Observations of landscape patterns can trigger a number of general questions: How do all these different patterns develop? What is the relative importance of different causes? Do similar patterns emerge from similar processes? How do landscape patterns change through time? What conditions produce gradual vs. abrupt changes in landscape patterns? Can future patterns be predicted? For how long are patterns discernible after the processes creating the patterns have ceased?

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DOI 10.1007/978-1-4939-2794-4_2

Contemporary landscapes result from many causes, including variability in *abiotic conditions*, such as climate, topography, and soils; *biotic interactions*, such as competition, mutualism, herbivory, and predation, that can generate spatial pattern even when environmental conditions are homogenous; *natural disturbances and succession*; and past and present patterns of *human land use*. Broad-scale variability in the abiotic environment sets the constraints within which biotic interactions and disturbances act. The environmental template sets the stage, but landscape patterns result from multivariate causes that operate and interact over many scales in time and space.

Long-term changes have been profound in many landscapes (Fig. 2.1), yet such changes are often underappreciated. Landscapes are constantly changing, each with a unique history. Many historical studies have provided data that lead to reinterpretations of the contemporary landscape (Foster 2002). Landscape ecologists must account for these long-term changes, and reconstructed landscape histories are an invaluable resource for clearer interpretation of contemporary patterns and dynamics. Determining how and why these histories developed is also critical for anticipating the future (Jackson 2006).

FIGURE 2.1.

This aerial view of Dubai illustrates a profound change in a desert landscape. *Source*: http://flagvruki.com/pictures/design-pic/dubay-s-vysoty-ptichego-poleta/

Exploring the causes of landscape pattern is not so easy as it may seem. Every landscape is unique because the observed spatial patterns result from multiple drivers and include both deterministic and stochastic processes. In a thought-provoking essay, Phillips (2007) developed an analogy between the "perfect storm," which refers to the improbable coincidence of several different factors or forces that produces an unusual outcome, and the "perfect landscape." The perfect landscape results from the combined, interacting effects of multiple environmental controls and drivers that generate a landscape unlikely to be duplicated at any other place or time. In other words, any particular landscape is a singular outcome from a range of plausible outcomes that depended on the occurrence or timing of different driving factors. This view of *multiple and contingent causation* supports an understanding of landscape pattern that allows for multiple outcomes rather than a single, deterministic result from a given set of conditions (Phillips 2007). Landscape patterns are idiosyncratic because of contingent factors that are particular in time and space. The critical observation that "it depends" complicates the task of explaining and predicting landscape patterns: similar landscapes may develop from contrasting trajectories, and different landscapes may have originated from similar initial conditions (Ernoult et al. 2006).

Contingencies that affect landscape patterns may be manifest in several ways. *Historical contingencies* exist when the current state of a landscape is clearly dependent on a specific past event or sequence of events. The term *landscape legacy* is often used to denote a persistent effect of past events or patterns on the contemporary landscape. *Spatial contingencies* exist when the state of a landscape depends on local conditions as well as the surrounding area. That is, characteristics at a given place also depend on characteristics at other locations, and thus changes at a particular location may be propagated spatially through the landscape (Phillips 2007). In practice, the reality of multiple interacting drivers and plausible outcomes means that elucidating the causes of landscape pattern remains surprisingly difficult (i.e., explained variance may be low), and predicting future patterns is not a trivial challenge.

Important information about the causes and changes in landscape patterns comes from the field of *paleoecology*, the study of individuals, populations, and communities of plants and animals that lived in the past and their interactions with changing environments. Paleoecology offers a wealth of insight into the long-term development of today's landscapes and has reestablished its ties with *biogeography*, which seeks to explain patterns of species distribution. One of the most important reasons for understanding landscape history is that we are in a period of rapid global change, and the past can provide us with important insights. We do not attempt a comprehensive review of this rich field, but we draw upon paleoecological studies to discuss the role of climate in the spatial structuring of the biota and the role of prehistoric humans in influencing landscapes. The *Holocene Epoch* (approximately the past 10,000 years) is of particular importance for understanding long-term landscape dynamics because it spans the current interglacial period. Studies in *environmental history* have also produced tremendous insights into how landscapes develop and change.

In this chapter, we discuss the general classes of factor that give rise to landscape patterns, provide a deeper temporal context for understanding present-day patterns, and elaborate the importance of landscape legacies. We then summarize some of the persistent challenges to explaining and predicting landscape change.

FOUR KEY DRIVERS OF LANDSCAPE PATTERN

The Abiotic Template

Landscape patterns develop on the template established by climate, landform, and soils. *Climate* refers to the composite, long term, or generally prevailing weather of a region (Bailey 2009), and climate acts as a strong control on biogeographic patterns through the distribution of energy and water. Climate effects are modified by *landform*—the characteristic geomorphic features of the landscape, which result from geologic process producing patterns of physical relief and soil development. Together, climate and landform establish the template upon which the soils and biota of a region develop.

CLIMATE

General climatic patterns will be familiar to all ecologists from introductory classes in biology or geography (readers might also consult Ruddiman 2008). At the broadest scale, climate varies with latitude, which influences temperature and the distribution of moisture, and with continental position. Because of differential heating of land and water, coastal regions at any given latitude differ from inland regions. The distributions of biomes on Earth result from these broad-scale climate patterns. However, the effects of both latitude and continental position are modified locally by topography, leading to finer scale heterogeneity in climate patterns (Bailey 2009). Temperatures generally decrease with increasing elevation, and north- and south-facing slopes experience different levels of solar radiation and hence different temperatures and evaporation rates.

Landscape ecologists must appreciate the importance of climate (and climate variability) as a driver of pattern. If the currently estimated magnitude of climate change is realized, climate-induced effects will profoundly alter landscape patterns and processes. Even in the absence of intensive human influences, the distribution of plant and animal communities and of entire biomes have varied tremendously with past changes in climate (Jackson 2006). The spatial distribution of today's life forms as a function of latitude/longitude looks quite different than those of 5000 or 10,000 years before present (BP). Furthermore, present assemblages of plants and animals represent only a portion of the ecosystem types that have existed during Earth's history, and future rates of change suggest that *"no-analog"* *communities* (i.e., communities that differ in composition from any that currently exist) will develop in the future (Williams and Jackson 2007). The Earth is warming rapidly in response to human-caused increases in greenhouse gases in the atmosphere, and this warming will continue into the foreseeable future (IPCC 2013). The rate and magnitude of expected climate change means that understanding climate as a driver will remain an active and critically important area for study, and we treat this topic in greater depth in Chap. 9. Already, studies have shown that organisms are rapidly shifting their distributions to higher latitudes and elevations (Chen et al. 2011); disturbance regimes are changing (Westerling et al. 2006); and permafrost, glaciers, and sea ice are melting (e.g., Perovich 2011). Thus, it is important for landscape ecologists to have a general understanding of climate variability and its potential effect on landscapes. We return to this topic in Chap. 9.

Earth's climate is dynamic. Glaciers have advanced and retreated several times during the past 500,000 years. Each glacial–interglacial cycle was about 100,000 years in duration, with 90,000 years of gradual climatic cooling followed by a period of rapid warming and 10,000 years of interglacial warmth. The peak of the last glacial period, or ice age, was about 18,000 years BP and ended approximately 10,000 years BP. These long climate cycles may be produced by cyclic changes in solar irradiance resulting from long-term and complex variation in Earth's orbital pattern (the Milankovitch Cycle) as the earth wobbles on its rotational axis (Crowley and Kim 1994; Overpeck et al. 2003). This orbital eccentricity results in approximately 3.5 % variation in the total amount of solar radiation received by earth and changes its latitudinal distribution.

During the past 150,000 years, the difference between the glacial and interglacial periods was described by a 5 °C shift in mean global temperature. To detect trends in the global climate system, climatologists remove spatial variability in climate by using mean global temperature, which is the only reliable expression of global surface air temperature. Thus, what may seem like small changes in mean global temperature can indicate very large fluctuations in temperature at many locations on Earth. For example, the *Medieval Warm Period* and the *Little Ice Age*, which lasted for >500 years, had large impacts on human populations and were only a 1 °C fluctuation in mean global temperature. Similarly, peak warming (about 1–2°C warmer than today) occurred between 9000 and 4000 years ago. This seemingly small increase led to a 70-km shift eastward in the prairie–forest boundary in the Upper Midwest (USA) compared to its present location. Recent studies suggest that direct and indirect effects of warming climate will result in "savannification" of the forest and once again shift this ecotone northward within the next 50–100 years (Frelich and Reich 2010).

An improvement in understanding the variability in Earth's climate and the ecological consequences of climate fluctuations has been documentation of global-scale climate anomalies, including the El Niño–Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), and Atlantic Multidecadal Oscillation (AMO).

ENSO and the PDO represent variation in sea-surface temperatures and sea-level atmospheric pressure in the equatorial and northern Pacific Ocean that, in turn, affect climate—especially drought—in western North America through midlatitude teleconnections (e.g., Diaz and Markgraf 2000). The AMO reflects slowly varying temperature patterns in the Atlantic Ocean. Drought and wetter-than-usual conditions in different regions are often associated with different phases of these climate anomalies. The La Niña phase of ENSO and warm phase of the AMO both contributed to the extreme 2010–2011 drought in Texas, USA (Nielsen-Gammon 2011). The combined cool phases of the PDO and ENSO (negative PDO during La Niña) are associated with drought and promote large fires in the southern Rocky Mountains, whereas the combined warm phases (positive PDO during El Niño) have such associations in the central and northern Rocky Mountains (Schoennagel et al. 2005). Future warming in the region is expected to increase the frequency of large fires and produce substantial increases in the area burned each year (Fig. 2.2).

The Earth's biota obviously must respond to climate fluctuations. Each species has a unique, multidimensional *fundamental niche*, defined as the environmental envelope within which viable populations can be maintained (Araújo and Guisan 2006). As climate fluctuates, the geographic distribution of environmental conditions that are suitable for any given species to survive and reproduce also shifts. In general, organisms may respond to climate change in three ways (Cronin and Schneider 1990), all of which contribute to long-term changes in their distribution: (1) organisms may evolve and speciate in response to changing patterns of selective forces; (2)

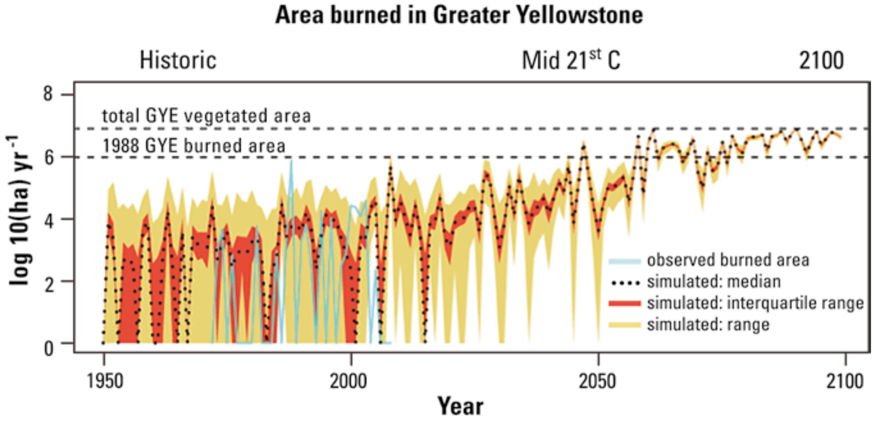


Figure 2.2.

Increased area burned associated with climate warming is projected for the Greater Yellowstone region of Wyoming, USA. Projected annual area burned (median, interquartile range, and full range) is shown here based on 1000 simulations using one global climate model through 2100. Area burned increases and years without fire decline substantially by midcentury.

Adapted from Westerling et al. (2011)

organisms may disperse and migrate to track suitable habitat, each according to its limits of tolerance and movement capability; or (3) species may become extinct if they neither adapt or move. Paleoecological research offers windows to the past by describing the vegetation patterns and shifts that accompanied past changes in climate. For example, classic research by Margaret Davis revealed that range limits of tree species in eastern North America changed dramatically during the past 13,000 years (Fig. 2.3) (Davis 1983). Species have varied not only in their ranges (i.e., the geographic area over which they occur), but also their local abundances—and thus relative dominance. For example, the range of oak (*Quercus*) in eastern North America expanded northward during the past 20,000 years, and the population centers where

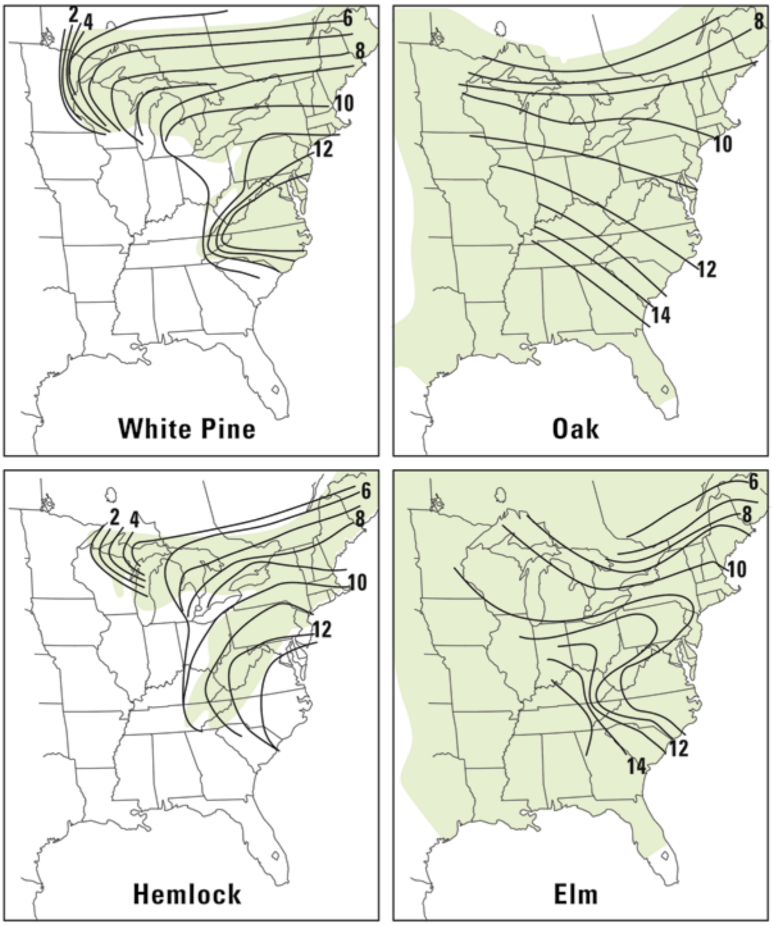


FIGURE 2.3.
Changes in northern and western range limits for four eastern North America tree taxa during the late Quaternary based on pollen records. Numbers indicate the time (in thousands of years before the present) at which pollen from each species was recorded at a given site. Shading indicates current geographic range.

ADAPTED FROM DAVIS (1983)

oak dominated the plant community also varied spatially (Delcourt and Delcourt 1987). More recent studies also provide examples from the paleoecological record of species assemblages that occurred in the Quaternary but are not observed today, and these co-occuring groups of species were often associated with no-analog climate conditions (Williams and Jackson 2007). The implication is that biotic assemblages of the future may be different from those observed in the past or present.

Although changes in mean climate through time are important, the influence of changes in climate variability is increasingly recognized (e.g., Thornton et al. 2014). Changes in the extreme values, such as maximum or minimum temperature or precipitation, may have large ecological effects, even if the mean value does not change. Increased variability could produce more record hot weather and more record cold weather with no change in mean temperature (Thornton et al. 2014). Extreme values may constrain where a particular species can survive or successfully reproduce. For example, in the Great Lakes region of the Upper Midwestern USA, declines in beech (*Fagus grandifolia*) populations occurred during times and locations of severe drought (Booth et al. 2012). Similarly, weather conditions at the tails of the distribution are often associated with infrequent severe disturbances, such as the very hot, dry conditions that are associated with large forest fires (Westerling et al. 2006). Recent decades have seen many records of maximum daily temperatures exceeded, especially during spring and summer. Such changes in climate variability are likely to have substantial impacts on food security, water supply, and other aspects of human well-being.

Climate is a driver of many natural disturbances (e.g., fire, floods, hurricanes, and landslides), and past changes in climate have altered disturbance regimes. For example, fire-return intervals in the Greater Yellowstone region (Wyoming, USA) varied between 100 and 300 years throughout the Holocene (roughly the past 10,000 years) in response to variability in climate (Millspaugh et al. 2000; Higuera et al. 2010). Similarly, the fire regime in northwestern Minnesota, USA, shifted from a 44-year fire cycle during the warm, dry fifteenth and sixteenth centuries to an 88-year fire cycle after the onset of cooler, moister conditions after 1700 AD and throughout the Little Ice Age (Clark 1990). At finer temporal scales, fire activity is also related to ENSO and PDO cycles (Schoennagel et al. 2005, 2007).

Several points that provide context for interpreting contemporary landscape patterns emerge from the many studies of past vegetation responses to climate. First, glacial–interglacial cycles have triggered the disassembly of communities followed by reassembly that is unpredictable in terms of either species composition or abundance. Compared to present-day communities, the past communities at many sites feature mixtures of species that are absent or very rare on the modern landscape (e.g., Barnosky et al. 1987; Williams and Jackson 2007). Second, the characterization of past plant communities indicates that the displacement of entire vegetation zones or communities is the exception rather than the rule. Species respond individualistically to climatic change, each according to its limits of tolerance, dispersal capability, and interactions with the surrounding biota. Third, disturbance regimes (discussed in detail in Chap. 6) have been very sensitive to past changes in climate. It is critically important for the landscape ecologist to appreciate the dynamic responses of the biota to variability in climate in space and time.

An important lesson from paleoecological studies is that climate has varied at nearly all ecologically relevant time scales, from among years to among millennia (Jackson 2004). The future implications of ongoing climate change for the distribution of Earth's biota and the patterns observed across landscapes are profound. The past decade has seen an exponential increase in the number and variety of studies that document changes that are already underway, with many species shifting northward and upward (e.g., Parmesan and Yohe 2003; Chen et al. 2011). Early evidence of recent climate change effects on tree distributions was detected in tree seedling distributions (Lenoir et al. 2009). For 13 of 17 tree species in French mountain forests, the elevation limit for seedlings was, on average, 29 m higher than the limit for adults (Lenoir et al. 2009). Many studies also forecast the potential ecological consequences of climate change (e.g., Coops and Waring 2011). The outputs from the suite of general circulation models and emissions scenario developed by the IPCC (e.g., IPCC 2013) form the basis for the vast majority of the forward-looking studies.

LANDFORM

Landforms range from nearly flat plains to rolling, irregular plains, to hills, to low mountains, to high mountains (Bailey 2009) and are identified on the basis of three major characteristics: (1) relative amount of gently sloping (<8 %) land, (2) local topographic relief, and (3) generalized profile, i.e., where and how much of the gently sloping land is located in valley bottoms or in uplands (Bailey 2009). Landforms may be described further by considering the topographic sequence of variation, or *soil catena,* of soils and associated vegetation types within each landform. For example, a mountainous landform may have a toposequence that includes ridgetops, steep slopes, shallow slopes, toe slopes, and protected coves. If different areas are composed of similar landforms with similar geology, then soil catenas and vegetation types may also be expected to be similar.

Four general effects of landform on ecosystem patterns and processes (Fig. 2.4) were categorized by Swanson et al. (1988) and still provide a useful classification:

1. *The elevation, aspect, parent materials, and slope of landforms affect air and ground temperature and the quantities of moisture, nutrients, and other materials available at sites within a landscape.* For example, south-facing slopes receive more solar radiation than northward slopes, resulting in warmer, drier conditions. These topographic patterns are strongly related to the distribution of vegetation across a landscape (e.g., Whittaker 1956). Locally, the degree of concavity or convexity may also be important in

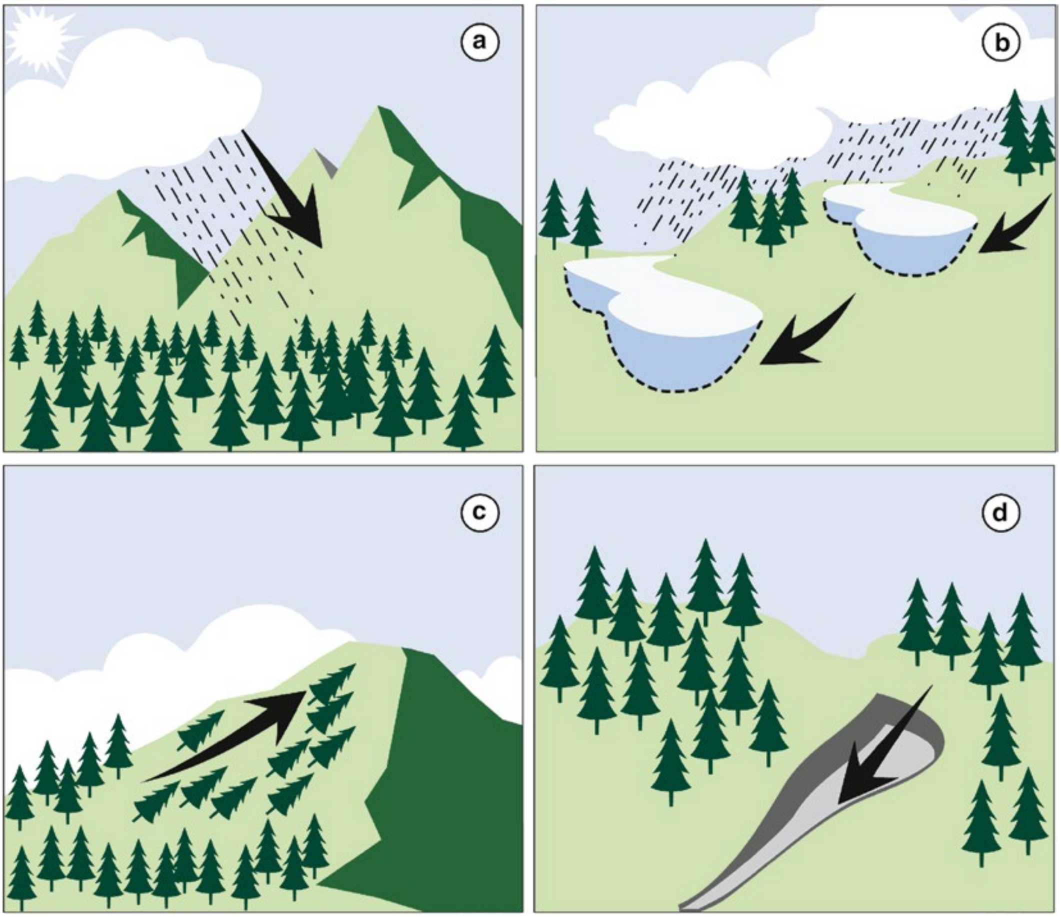


Figure 2.4.

Examples of four classes of landform effects on ecosystem patterns and processes. (**a**) Topographic influences on rain and radiation (*arrow*) shadows. (**b**) Topographic control of water input to lakes. Lakes high in the drainage system receive a greater proportion of water input by direct precipitation that lakes lower in the landscape, where groundwater (*arrows*) predominates; also see Chap. 9. (**c**) Landform-constrained disturbance by wind (*arrow*) may be more common in upper-slope locations; also see Chap. 7. (**d**) The axes of steep concave landforms are most susceptible to disturbance by small landslides (*arrow*).

Modified from Swanson et al. (1988)

determining microclimate or the rates of organic matter accumulation, and a landform index (also called a terrain shape index) is often used to characterize such local topographic variation (e.g., McNab 1993; Abella 2007). Methods also exist for estimating temperature variability in areas of complex terrain, such as mountainous environments, by explicitly accounting for topography (e.g., Lookingbill and Urban 2003). These methods are very useful because measurements at a single location (e.g., a weather station) cannot represent all locations in a topographically complex landscape with accuracy, and models that distribute such measurements at finer scales within a landscape are needed.

2. *Landforms affect the flow of many quantities, including organisms, propagules, energy, and matter through a landscape.* The funneling of winds, for example, may lead to dispersal pathways for wind-blown seeds. Many animal species have been observed to travel along riparian corridors (e.g., forest birds in tropical forests, Gillies and St. Clair 2008; wildlife along rivers, Naiman and Rogers 1997), and such corridors are also important for hydrochorous seed dispersal (e.g., Dixon et al. 2002). The position of lakes relative to groundwater flow pathways can strongly influence the chemical and biological characteristics of those lakes (Martin and Soranno 2006; Lottig et al. 2011). Fires are known to burn more rapidly in the upslope rather than downslope direction (e.g., Johnson and Miyanishi 2001).
3. *Landforms affect the frequency and spatial pattern of natural disturbances such as fire, wind, or grazing.* Across a New England landscape, susceptibility to damage from hurricanes varied with landscape position, with greater damage observed in more exposed topographic positions (Foster and Boose 1992; Boose et al. 1994). In coastal forests in Alaska, patterns of windthrow were also strongly influenced by topographic position (Kramer et al. 2001).
4. *Landforms constrain the spatial pattern and rate or frequency of geomorphic processes—the mechanical transport of organic and inorganic material—that alter biotic characteristics and processes.* Many different kinds of transport processes (e.g., by wind or water) move materials around landscapes (Reiners and Driese 2004) and are influenced by landform. Portions of a landscape may be more or less susceptible to landslides or to shifts in river channels.

Taken together, landforms significantly contribute to the development and maintenance of spatial heterogeneity across a landscape through their multiple effects on soils, vegetation, and animals (Swanson et al. 1988). Even in areas of relatively little topographic relief, such as the glacial landforms of the Upper Midwest of the US or riparian floodplains, physiography contributes to spatial variability in vegetation patterns (e.g., Turner et al. 2004a).

Soils

In terrestrial environments, soils provide the mineral nutrients, water, and support medium required by the vegetation. The substrate and soils of the surrounding landscape also affect the chemical qualities of the water in aquatic systems. Although it may be associated with particular landforms, there is tremendous spatial variability in *parent material* (i.e., the unweathered geologic material from which soil develops) across the surface of the Earth. Soils form, in part, through the process of weathering, in which chemical dissolution and physical abrasion break down parent materials. Microbial activity is also important, and plant roots play an important role in soil formation. Soils are important in explaining landscape patterns because they differ substantially in many physical and chemical characteristics (e.g., texture, depth, pH, mineral composition) that influence the species that can be supported. For example, soils have different water-holding capacities, nutrient concentrations, and organic matter content, and such differences can lead to dominance by different plant species. In his classic plant ecology studies, Curtis (1959) described variation in plant communities or Southern Wisconsin that were associated with a soil-moisture gradient—mixed hardwoods on moist soils; *Acer* and *Tilia* on well-drained mesic sites, and a series of *Quercus* species on progressively drier sites.

Studies of ecosystem development on Hawaii have provided convincing evidence for the role of substrate age on landscape patterns. Volcanic lava flows have occurred at varying times in the past, providing a unique opportunity to study ecosystem development on substrates of different age. Nutrient availability changes with long-term soil development (Vitousek and Farrington 1997). Young substrates (300 years BP) are relativity rich in available phosphorus, but plant growth is limited by relatively low nitrogen availability. Mineral phosphorus declines with substrate age, with nitrogen and phosphorus equilibrating in substrates of intermediate age. Eventually, plant growth becomes limited on old substrates (>150,000 years BP) by declining levels of phosphorus (Vitousek and Farrington 1997). These differences in soil development are, in turn, associated with substantial variation in forest structure and disturbance dynamics (Kellner et al. 2011). Although Hawaii offers a somewhat unique set of conditions, the general point is that substrate and soils have strong influences on vegetation and thus landscape structure. It is very important to understand these influences.

Biotic Interactions

Interactions among organisms—both positive and negative, such as competition, predation, and facilitation—can lead to spatial structuring of populations even when environmental resources are homogeneous in space. Theoretical population ecology focuses much attention on these dynamics (Tilman and Kareiva 1997; Ives et al. 1998), with an emphasis on how biotic interactions within and among populations can generate spatial patterns, and how these patterns, in turn, influence the outcome of further interactions. The product of these theoretical approaches often is a map of species distributions, or a time series of how these distributions may change in time and space.

COMPETITION

Competition between two species in a landscape without any abiotic variation theoretically could result in homogeneous spatial distribution (i.e., one species remaining) through competitive exclusion (Gause 1934). The best competitor would win out and establish itself throughout the landscape, resulting in a homogeneous distributional pattern. However, there are important exceptions to competitive exclusion.

Groups of competing organisms may interact in complex ways so that final distributions take on one of many alternative stable states. These *multiple stable states* (Sutherland 1974) may often occur when several different species can potentially occupy and dominate a site. Which species actually occurs on a specific site is determined by very small, stochastic changes in the initial conditions. But once established, the abundance pattern (and hence, the community state) may persist for many generations in spite of minor disturbances. However, a major disruption can shift abundance patterns and produce a new configuration that is also stable. This type of shifting, stochastic pattern is often observed near ecotones between major community types. For example, small, stable stands of trees may extend out into grassland, and small stable patches of grasses may intrude into the forest. Along this ecotonal edge, both communities are stable, and there are very small differences in the competitive advantage of one community over the other. Chance plays a role in which community is established, and once established that community can maintain itself until a major disruption occurs.

Gradients in resources, combined with competitive actions between species, can result in sudden shifts in vegetation types, or ecotones, even when the environmental resource gradients are small (Fig. 2.5). Along a north–south transect, for example, temperature and moisture may change gradually and continuously, with no sharp discontinuities. Conditions to the south may favor one species, while conditions to the north favor another. Somewhere along the transect, conditions will be suitable for the growth of both species. Competition for space may form a sharp ecotone between them, rather than a gradation or intermingling. Resource gradients may also influence mutualisms, such as plant–pollinator interactions, in ways that can produce spatial patterns. For example, the relative abundance of different flower morphologies varies along gradients of elevation and climate in response to variation in pollinator availability (Pellissier et al. 2010).

A different sort of pattern emerges from *reaction-diffusion* models of interacting populations (Okubo 1975). In these models, growth and competition occurs while species are also dispersing across a uniform environment. In many cases (Levin 1978), the initial uniform distribution of species is destabilized by the random diffusion, and the system spontaneously assumes a patchy, but periodic spatial distribution. For example, in *predator–prey models*, a patchy distribution results if the diffusion rate of the predator is sufficiently greater than that of the prey. A fixed spatial pattern with peaks and troughs in the density of both predators and prey can emerge with time. This mechanism of *diffusive instability* has been suggested as the cause of patchy distribution in plankton (Kierstad and Slobodkin 1953; Steele 1974a; Edelstein-Keshet 1986; Murray 1989). We might suspect this type of mechanism whenever a periodic or quasi-periodic pattern is detected on the landscape.

Figure 2.5.
Very slight differences in topography in the glaciated landscape of northern Wisconsin, USA, lead to substantial differences in soil water, creating a distinct ecotone between bog vegetation and upland forest.
Photo by M. G. Turner

Pattern also results from the activities of a *keystone species*. Paine (1974, 1976) studied the interactions between the mussel *Mytilus californianus* and its starfish predator, *Pisaster ochraceous*, in the intertidal zone. The mussel is a superior competitor, but predation by the starfish keeps the mussel population in check. Higher up on the shoreline, the starfish has difficulty reaching the mussels. The mussels completely dominate the rock surfaces and eventually grow too large for the starfish to handle. Further down the shoreline, the starfish consumes all young mussels. The result is a very distinct striped pattern on the rocks, with mussels above, but not below this line. When Paine (1974) experimentally removed the starfish, the mussels moved down the surface of the rock, outcompeting and eliminating 23 other species of invertebrates. The starfish is clearly the keystone predator that creates and maintains the spatial pattern. Holling (1992) believes that keystone species and processes are a common cause of pattern, stating that, "All ecosystems are controlled and organized by a small number of key plant, animal, and abiotic processes that structure the landscape at different scales."

Influence of Dominant Organisms

In many respects, it is the dominant species that define spatial pattern on the landscape. Such organisms have been termed *foundation species*: a single species that defines much of the structure of a community by creating locally stable conditions for other species, by providing habitat, and by modulating and stabilizing fundamental ecosystem processes such as nutrient cycling (Ellison et al. 2005). Within the context of the abiotic template, foundation species alter the abiotic conditions and provide a resource base and substrate for the other populations in the ecosystem. This is not only true in terrestrial ecosystems; for example, kelp is the foundation species in some coastal ecosystems, and corals can be foundation species along tropical shorelines. The coral forms the substrate and resource base for the entire food web and its spatial distribution dictates the spatial pattern for the rest of the ecosystem.

Another source of landscape pattern derives from the activities of *ecosystem engineers*, organisms that physically create or modify habitat structure (Wright and Jones 2006). A notable example of an ecosystem engineer is the beaver (*Castor canadensis*), which alters riparian landscapes in much of North America. The beaver uses sticks and mud to dam a second- to fifth-order stream, impounding water behind the dam (Johnston and Naiman 1990a) and altering riparian vegetation and soils, forming extensive wetland mosaics. Aerial photography shows that as much as 13 % of the landscape can be altered in this way (Johnston and Naiman 1990b). Beaver activity increases landscape heterogeneity and can increase the number of herbaceous species in the riparian zone by over 33 % (Wright et al. 2002). In the northern portions of Yellowstone National Park, a decline in the stature and abundance of willows (*Salix* spp.) during the twentieth century was linked to reduced beaver activity (Wolf et al. 2007). Hydrologic changes, stemming from competitive exclusion of beaver because of overbrowsing by elk (*Cervus elaphus*), may have caused the landscape to transition from a historical beaver-pond and willow-mosaic state to an alternative stable state where active beaver dams and many willow stands are absent (Wolf et al. 2007). Recovery of willow in the landscape thus may depend on recovery of a key ecosystem engineer. A variety of other examples of ecosystem engineers creating landscape pattern include the American bison (Knapp et al. 1999), earthworm (Holdsworth et al. 2007), and white rhinos (Waldram et al. 2008).

LANDSCAPE CONSEQUENCES OF TROPHIC CASCADES

The concept of *trophic cascades* emerged from studies of within-lake communities and referred to the control exerted by a predator's influence "cascading" down the food chain (Carpenter et al. 1985). In landscape ecology, trophic cascades have been considered in the context of predators influencing the spatial patterns of herbivore presence or abundance, which can in turn affect vegetation patterns. Predators may affect herbivores directly by consuming them, or indirectly (i.e., nonconsumptive) by creating a *landscape of fear* that causes herbivores to alter their behavior. If herbivores avoid riskier areas of the landscape and use safer locations, the distribution and/or abundance of forage plants may also change. Thus, predators can initiate spatial trophic cascades by consuming and/or scaring their prey. Such dynamics were hypothesized in northern Yellowstone National Park, USA, following the 1995 reintroduction of wolves (*Canis lupus*) (e.g., Laundre et al. 2001), a landscape in which large populations of elk have been implicated in constraining the distribution of preferred browse species including aspen (*Populus tremuloides*) and willow (*Salix* spp.). After considerable study, some authors concluded that wolf reintroduction restored behaviorally meditated trophic cascades that allowed woody vegetation to grow taller and canopy cover or stem growth to increase in some locations (Beyer et al. 2007; Ripple and Beschta 2012). Other authors, however, found no evidence for recovery of aspen or willow, even where wolf populations were high (e.g., Creel and Christianson 2009; Kauffman et al. 2010; Kimball et al. 2011). The spirited scientific discussions surrounding this topic reflect the excitement associated with integrating behavioral ecology and trophic cascades as they may jointly affect landscape patterns.

Human Land Use

Patterns of land use can alter both the rate and direction of natural processes, and land-use patterns interact with the abiotic template to create the environment in which organisms must live, reproduce, and disperse. *Land use* refers to the way in which, and the purposes for which, humans employ the land and its resources (Meyer 1995). For example, humans may use land for food production, housing, industry, or recreation (Nir 1983). A related term, *land cover,* refers to the dominant habitat or vegetation type present, such as forest and grassland. Although they are related, it is important to note the distinction between these terms: an area of forest cover may be put to a variety of uses including low-density housing, logging, or recreation. We use "land-use change" to encompass all those ways in which human uses of the land have varied through time. The ways in which humans use the land are important contributors to landscape pattern and process.

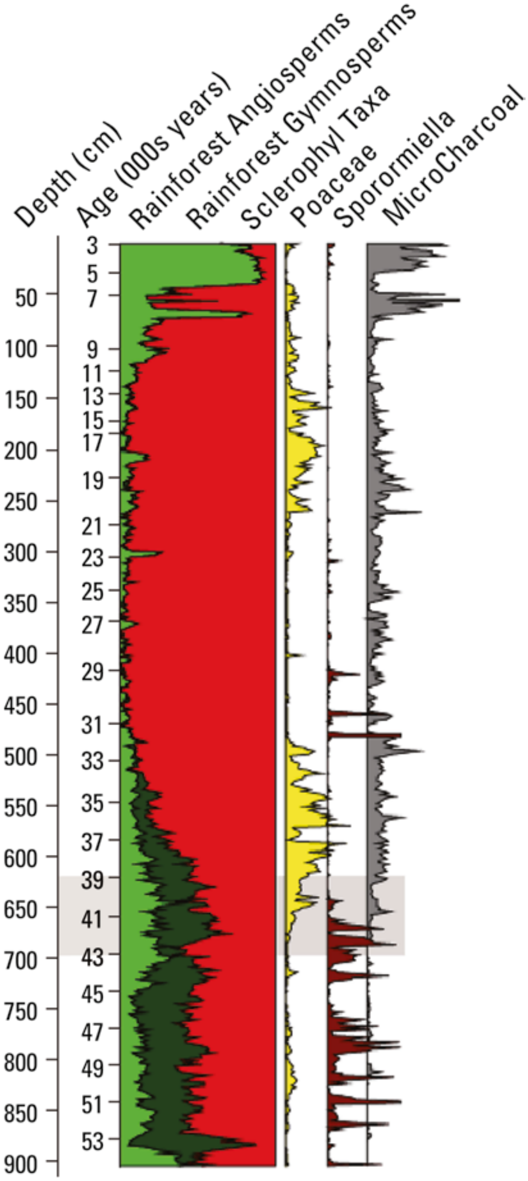
Prehistoric Influences

Prehistoric humans had a major role in influencing landscapes (Fig. 2.6), and their past effects contribute to present-day landscape patterns. Using the pollen record, indications of human activities can be traced back thousands of years, and discrete episodes of human disturbance can be correlated with archeological data. Consider, for example, the historical expansion of human influences in Europe (Delcourt and Delcourt 1991). In the early Holocene, there was broad-based foraging throughout the Mediterranean region. The switch from a nomadic to a more sedentary way of life was just beginning ~10,000 BP, and by ~800 BP, when permanent settlements were established in Greece. These settlements included cultivation of crops and maintenance of livestock, and food production became more

Figure 2.6.

Using a high-resolution 130,000-year environmental record, Rule et al. (2012) helped to resolve the cause of extinction of Australia's megafauna. Results suggest that human arrival rather than climate caused megafaunal extinction, which then triggered replacement of mixed rainforest by sclerophyll vegetation through a combination of direct effects on vegetation of relaxed herbivore pressure and increased fire in the landscape. This ecosystem shift was as large as any effect of climate change over the last glacial cycle and indicates the magnitude of changes that may have followed megafaunal extinction elsewhere in the world.

Modified from Rule et al. (2012)



labor intensive. Cereal cultivation caused a major shift in patterns of land use because the permanent fields needed weeding and required nutrient replenishment, both of which were activities requiring considerable human labor. By about 6500 BP, farming expanded north of Greece as winters became warmer and precipitation increased. Development of more efficient technologies also contributed to the continued expansion of agriculture in Europe. Use of the "ard," a tool that used the angle between the trunk and roots of a tree to break through the soil and which was pulled by an oxen, became prevalent ~5000 BP. Further human expansion became based on the maintenance of work animals because oxen-drawn plows that could both furrow and turn over the soil were developed and used by ~3000 BP. More efficient bronze sickles also replaced wooden sickles.

What were the effects of this expansion of human activities in Europe on native vegetation? The impact of the axe and spade on ecosystems began to transform natural landscapes into cultural ones through plowing, burning, and trampling. The ard, because it did not overturn the soil, left perennial roots intact. The plow, however, removed perennials from the soil and encouraged establishment of annual plants. The process of deforestation and conversion of land to pasture or crop cultivation changed the landscape from a natural to a cultural mosaic (Delcourt 1987). This also occurred in North America, although early settlements of Native Americans were more restricted to floodplains; uplands were used much later than in Europe (Delcourt 1987). However, Native Americans in North America profoundly influenced the landscape by establishing settlements, practicing agriculture, hunting, and using fire to induce vegetation changes (Denevan 1992).

The influences of prehistoric humans on landscapes were characterized by Delcourt (1987) into five main types. (1) Humans changed the relative abundances of plants, especially the dominance structure in forest communities. In the pollen record from Crawford Lake, Ontario, land clearance and maize cultivation by the Iroquois is documented by pollen sequences spanning the fourteenth to seventeenth centuries. During this time, the dominance of tree species in the surrounding forest changed from late-successional species such as beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) to forest of oak (primarily *Quercus rubra*) and white pine (*Pinus strobus*). (2) Humans extended or truncated the distributional ranges of plant species (woody and herbaceous). In Europe, for example, the range of olives (*Olea europaea*) after 3000 years BP was extended through cultivation from the Mediterranean coast throughout southern Europe. Truncation of the range of a native tree species by prehistoric humans has been documented for bald cyprus (*Taxodium distichum*) in the central Mississippi and lower Illinois valleys in eastern North America. Charcoal evidence suggests a preference for cyprus wood during the period from 2000 years BP to 1450 AD, with the species becoming locally extinct as human populations increased (Delcourt 1987). (3) Opportunities were created for the invasion of weedy species into disturbed areas. In many places, weedy species assemblages associated with cultivated fields increase in abundance in the pollen record, and these increases are correlated with archeological evidence of human occupation (Delcourt 1987). (4) The nutrient status of soils was altered through both depletion and fertilization. (5) The landscape mosaic was altered, especially the distribution of forest and nonforest. This last change is also easiest to detect in the paleoecological record by examining ratios of tree to herbaceous pollen.

A key point from this brief discussion of long-term development of the cultural landscape is that what we perceive to be “natural” today may be, in fact, the product of human alterations that date back over several centuries. For instance, one can still see the imprint of Roman roads when fields lie fallow in Belgium. A wide range of ecosystem effects due to human activities may be found, from harvests of resources, agricultural development, and urban construction. Because humans have long been present in many landscapes, their role in creating landscape pattern should not be discounted.

Historical and Present-Day Effects

Both worldwide and in the United States, land-cover patterns today are altered principally by direct human use: by agriculture, raising of livestock, forest harvesting, and construction (Meyer 1995). Human society relies on natural habitats for a variety of services, including productivity; recycling of nutrients; breakdown of wastes; and maintenance of clean air, water, and soil. In North America, land-use changes have been particularly profound since Europeans settled the continent three centuries ago. Landscapes have become mosaics of natural and human-influenced patches, and once-continuous natural habitats are becoming increasingly fragmented (e.g., Burgess and Sharpe 1981; Harris 1984).

Land-use changes in the United States serve as a handy example. At the time of European settlement, forest covered about half the present lower 48 states. Most of the forestland was in the moister east and northwest regions, and it had already been altered by Native American land-use practices (Williams 1989). Clearing of forests for fuel, timber, and other wood products, and to open the land for crops led to a widespread loss of forest cover that lasted through the early 1900s. So extensive was this loss that by 1920 the area of virgin forest remaining in the conterminous United States was but a tiny fraction of that present in 1620 (Fig. 2.7). Some originally cleared areas, for example, New England, the Southeast and the Upper Midwest, have become reforested due to lack of cultivation. In other regions, clearing for agriculture has been more permanent (e.g., the Lower Midwest), or harvest of primary forest has continued until recent times (e.g., Pacific Northwest).

Through their activities, modern humans have often been shown to simplify landscape patterns, creating straighter and more regular spatial arrangements (Krummel et al. 1987). Roads, transportation corridors, and other linear features impose new spatial patterns in landscapes (e.g., Laurance et al. 2009; Forman et al. 2003). Urbanization results in profound changes to aquatic systems, burying first-order streams (Elmore and Kaushal 2008), replacing vegetation that shades stream corridors and prevents erosion (Baron et al. 1998) with hardened surfaces producing high-intensity flows that transport greater levels of sediment and nutrients (Lookingbill et al. 2009).

Developed land in the United States has expanded as the population has grown in number, with most of the population now living in cities, towns, and suburbs rather than on farms. Americans spread out more across the land as transportation technologies improved, especially as the automobile became the primary mode of

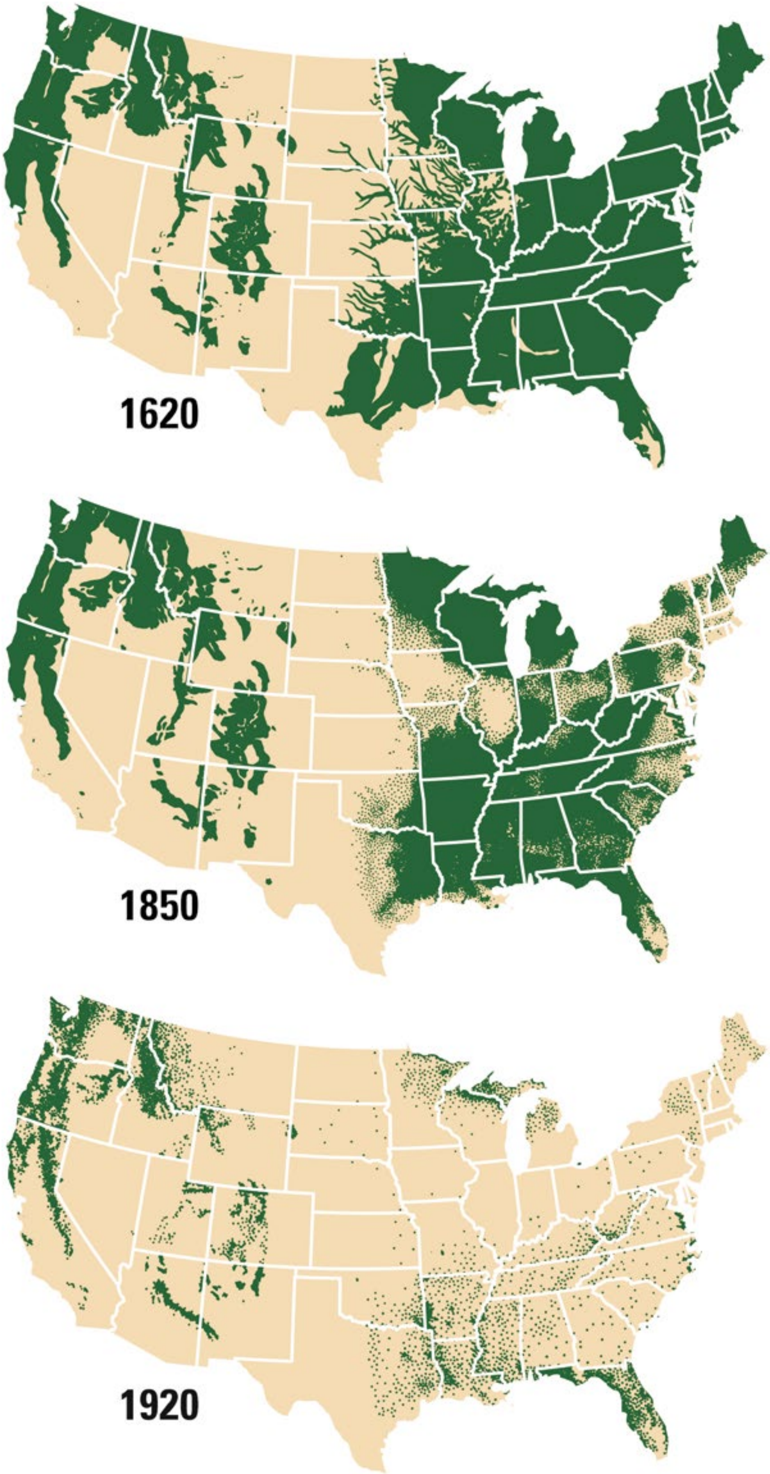


FIGURE 2.7.
Approximate area of virgin old-growth forest in the contiguous United States in 1620, 1850 and 1920. Note that this does not depict total forest area because many forests, especially in the eastern United States, have regrown following clearing and the abandonment of agriculture.

ADAPTED FROM MEYER (1995)

transportation. Present-day patterns of settlement take up more land per person than in the past, and homes and subdivisions are more dispersed across the landscape. Exurban development has increased in many North American landscapes as environmental amenities attract residents to more rural areas. The resulting increase in the *wildland–urban interface* (WUI) has received considerable attention (e.g., Radeloff et al. 2005; Theobald and Romme 2007). The consequences of increased residential development in forested regions (i.e., houses under the canopy) are not well understood but are receiving considerable study. Expansion of the WUI is associated with increasing conflicts between human values and ecological processes, such as natural disturbance and activities of large predators.

Urbanization is a strong trend globally, and a frontier of rapid and sometimes chaotic land-use change surrounds urban areas (Meyer 1995; Mcdonald et al. 2009). For example, changes in landscape pattern around Beijing, China, show increased fragmentation associated with the concentric rings of expanding urbanization (Shi et al. 2012). Trends in urban land are unique because they typically run in only one direction—that is, urban lands do not revert readily to other categories in the short term. Thus, the distribution of developed lands will leave a long-lasting footprint on the landscape (Turner et al. 1998a), and proximity to urban lands is strongly associated globally with increased threats to conservation lands (Mcdonald et al. 2009).

EMERGENCE OF THE ANTHROPOCENE

The pervasive influence of humans on landscapes throughout the world is widely recognized, and there is growing consensus that humans have transformed ecosystem patterns and processes across most of the terrestrial biosphere (e.g., Foley et al. 2005). This recognition has led some researchers to suggest that the traditional depiction of global biomes based on climate and physiography is insufficient to depict the patterns of terrestrial ecosystems. Ellis and Ramanukutty (2008) introduced the concept of anthropogenic biomes, or *anthromes*, to assess the human-caused changes in the classic biomes. Globally, anthropogenic transformations of biomes between 1700 and 2000 resulted about equally from land-use expansion into wildlands and from intensification of land use (Fig. 2.8; Ellis et al. 2010a, b) See following note in figure legend. These authors report that the terrestrial biosphere made a critical transition from mostly wild to mostly anthropogenic early in the twentieth century (Ellis et al. 2010a, b). For landscape ecologists, it is clear that human activities and land use must be considered a key driver of landscape pattern.

Disturbance and Succession

Disturbance and the subsequent development of vegetation are key contributors to pattern on the landscape. By *disturbance*, we mean any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource availability, substrate, or the physical environment (White and Pickett

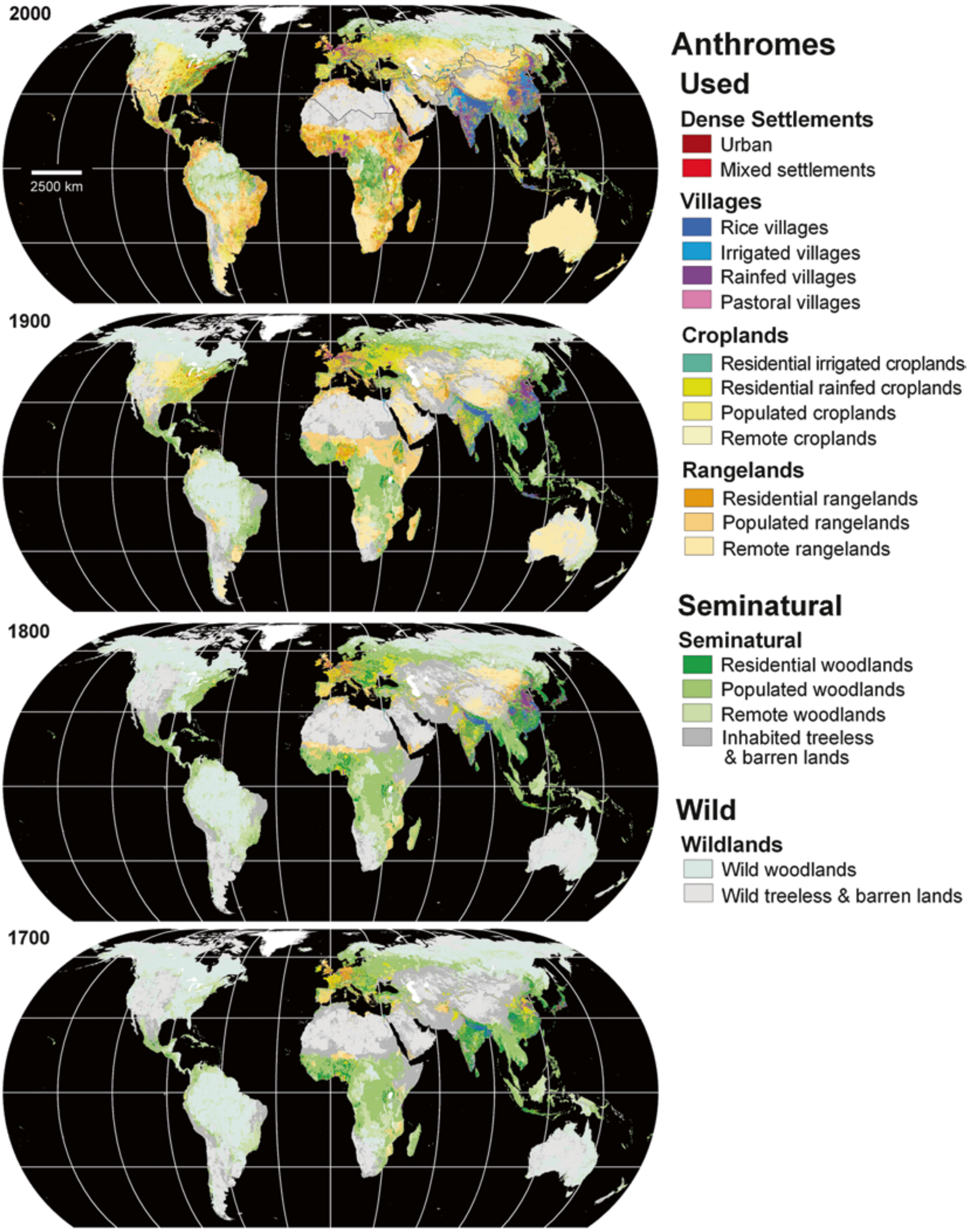


FIGURE 2.8.

Anthropogenic biomes and changes in their global distribution between 1700 and 2000.

From Ellis et al. (2010b) and available at http://ecotope.org/anthromes/maps/

1985). Examples include fires, volcanic eruptions, floods, and storms. Disturbances are often described by a variety of attributes including their spatial distribution, frequency, spatial extent, and magnitude. The spread of disturbance and spatial patterns of recovery have received considerable attention in landscape ecology, and we devote a chapter to exploring these dynamics (see Chap. 6). Here, we briefly recognize disturbance as an important agent of pattern creation at a variety of spatial and temporal scales. As with the other factors discussed in this chapter, disturbances leave a heterogeneous imprint on terrestrial landscapes (e.g., Foster et al. 1998; Turner 2010) as well as within aquatic systems, such as riverine landscapes (e.g., Parsons et al. 2005).

LANDSCAPE LEGACIES AND THE ROLE OF HISTORY

A major development in contemporary landscape ecology has been confirmation of the role of history in today's landscapes and the widespread importance of landscape legacies. Since the 1980s, this recognition has grown along with the rise of environmental history (e.g., Cronon 1982) and an early recognition in ecology that history might explain contemporary patterns. Many scientists thought that the distant past had little effect on modern ecosystem patterns and processes (Foster et al. 2003). However, when ecological studies expanded to regional scales, it became difficult to avoid consideration of current and historical human activities—the role of people could no longer be ignored. There was also growing evidence that most "natural areas" had more cultural history than had been assumed previously, and there was acknowledgement that the legacies of historic land use were remarkably persistent. Finally, there was appreciation that history adds explanatory power to understanding the structure and function of contemporary landscapes. Numerous empirical studies have now documented effects of historical events on a wide range of attributes (e.g., species presence and abundance, forest stand structure, nutrient pools and fluxes, and vulnerability to nonnative invasive species). Vegetation and soils seem to be particularly sensitive indicators of historic land use. Although historic timber harvesting and agriculture [i.e., "the *ghost of land use past*" (Harding et al. 1998)] have received most attention, natural disturbances can also leave their mark on landscape patterns for decades or even centuries.

In well-developed forests of the northeastern US, David Foster and colleagues found that variation in soil characteristics and the plant community reflected land use that occurred over 100 years ago (Foster 1992). Although the regional distribution of forests was similar to that of presettlement, some tree species (e.g., birch, red maple) had increased over time while others (e.g., sugar maple, beech) had declined. Their analyses showed that the variety and abundance of trees varied with past land use. Indeed, despite environmental variation in the region, studies have shown that the extensive nineteenth-century forest clearance and land use resulted in severe reductions or local extinction of forest plant populations and remains an overriding factor influencing modern vegetation composition and structure (Bellemare et al. 2002). In northern US Great Lakes forests, historical land use was associated with homogenization of forest communities across the landscape, and current forests that have lower species diversity, functional diversity, and structural complexity compared to pre-Euro-American forests (Schulte et al. 2007). In forests of the southern Appalachians, the legacies of historic land use also affected the likelihood that forest understories might be invaded by nonnative species (Kuhman et al. 2010).

Effects of historical land use were especially pronounced on forest herbs that have limited dispersal capability, a trend also reported in other regions (e.g., Southern Appalachians, Pearson et al. 1996; Mitchell et al. 2002; Ontario, Canada, Brown and Boutin 2009). While effects of historical agriculture on forest understory plants are partly mediated by establishment limitation (Flinn and Vellend 2005), mortality of seedlings and juveniles may also be higher in more recent forests (Jacquemyn and Brys 2008). Biomass allocation patterns also can differ with historical land use (Fraterrigo et al. 2006a). Soil nutrient concentrations sometime vary with land-use history (e.g., Bellemare et al. 2002), and Fraterrigo et al. (2005) found that historical land use altered the variance and spatial structure of soil nutrients. Soil microbial communities also showed a persistent legacy of land use history (Fraterrigo et al. 2006b). Geostatistical analyses (which are covered in Chap. 5) suggested that the spatial patterns of soil carbon, potassium, and phosphorus were homogenized in former pastures (Fraterrigo et al. 2005). Carbon storage can also be affected by land-use history. In Wisconsin, USA, total aboveground live forest carbon declined by nearly 75 % between presettlement times and the peak of agricultural clearing in the 1930s (Rhemtulla et al. 2009). Carbon stocks recovered subsequently to about 60 % of the presettlement value, but the landscape distribution of carbon storage shifted. Former savanna ecosystems in the south store more carbon, and forest ecosystems in the north store less (Rhemtulla et al. 2009).

In addition to the actual use land in the past, the spatial pattern of historic land use can influence contemporary patterns. In seminatural grasslands in Sweden, the spatial configuration of habitats in the landscape influenced plant species diversity for 50–100 years (Lindborg and Eriksson 2004). Species diversity was not related to current connectivity of the grasslands, and strong relationships were found with the historic patterns of the grasslands. Historic connectivity was positively related to estimates of species diversity, the total species richness, and species density, and the model with the highest explanatory power included the configuration from 100 years ago (Lindborg and Eriksson 2004). This study demonstrated that present-day species composition was related to historic landscape structure and suggested time-lagged influences of historical habitat patterns. Other studies have demonstrated similar consequences of historical habitat connectivity on contemporary species assemblages, including butterflies in European grasslands (Sang et al. 2010) and understory plants in pine woodlands on the coastal plain of the southeastern US (Brudvig and Damschen 2011).

For how long do land-use legacies persist? The answer varies among landscapes, of course, but studies in western Europe have revealed exceptionally long land-use legacies. In northeastern France, large areas were cleared of forest during Roman occupation, farmed, and then abandoned to forest. Using archeological evidence to reconstruct land-use patterns, Dupouey et al. (2002) tested the hypothesis that legacies of the ancient agriculture may last for millennia. The data supported this hypothesis: plant community composition was closely related to the intensity of ancient land use (Dupouey et al. 2002). These authors concluded that 200 years of farming during Roman times induced gradients in soil nutrients and plant assemblages that were still measurable almost 2000 years later! Further, the effects of Gallo-Roman occupation 1600 years ago were observed not only on current-day soils and plant communities but also in the seed bank (Plue et al. 2008). Historic land use was associated with persistent ruderal species in the seed bank, co-occuring with several ancient forest species that were at high abundance in the occupied sites. Clearly, the impact of ancient land use on forest vegetation in Europe must not be underestimated (Plue et al. 2008).

We have emphasized land-use legacies, but natural disturbances can also produce persistent legacies through their influence on spatial patterns of postdisturbance succession. Disturbances themselves produce patterns (e.g., Foster et al. 1998), and a stand-age mosaic is often observed across a landscape that has been subjected to disturbances at different times in the past. However, a single disturbance event can also create a long-lasting imprint on landscape pattern. Following the 1988 fires in Yellowstone National Park, WY, studies reported enormous variation in postfire stand density (0 to >500,000 stems ha^{-1}) within the burned landscape (Turner et al. 2004b). Chronosequence studies used to reconstruct the spatial variability of tree density in the past revealed that postfire variation in stand structure and function persists for nearly 200 years (Kashian et al. 2005a, b).

In sum, landscape legacies are ubiquitous and important. Current studies continue to explore the role of history, and many questions remain to be explored. For example, variation in agricultural practices (e.g., tillage, crop rotations, fertilizer applications) often is not well resolved in space or time, and arid lands can be more difficult to study. How do historical legacies constrain restoration alternatives? Under what conditions can reintroduction of historically natural processes (e.g., fire) restore historic landscape conditions? What will be the future legacies of today's patterns of land use?

WHY IS IT STILL DIFFICULT TO EXPLAIN AND PREDICT LANDSCAPE CHANGE?

At the beginning of this chapter, we claimed that predicting landscape change remains very challenging. It is much easier to explain patterns by looking back in time than it is to anticipate future rates, directions, and spatial patterns on a given landscape. Why does this remain so difficult? What approaches are useful? Returning to the notion of the perfect landscape, Phillips (2007) summarized three take-home points that we paraphrase here for landscape ecologists:

1. A landscape at a given place and time is a particular, contingent outcome of deterministic, global laws operating in a specific environmental and historical context. Historical and spatial contingencies are very important, and landscape patterns may converge or diverge over time.
2. A given landscape is only one possible outcome of a given set of processes and boundary conditions, which is determined by a specific, perhaps irreproducible set of contingencies. However, the possible outcomes are constrained by deterministic controls that set boundaries on what outcomes are feasible.
3. Explaining landscape patterns requires the integration of global approaches that consider the deterministic controls and local approaches that account for the contingencies.

From this, it follows that predicting future landscape patterns is difficult because contingencies may be unanticipated or even unpredictable. When similar locations can arise from different histories, and similar histories can produce different outcomes (e.g., Ernoult et al. 2006), it is not easy to infer causation. Here, we highlight four key factors that make prediction landscape patterns difficult.

Multivariate Interacting Drivers

Landscape patterns are clearly not the result of single drivers. Multiple drivers are often operating across a wide range of spatial and temporal scales, and they may interact in unpredictable ways.

Statistical methods are increasingly employed to detect multivariate correlates of changing patterns (e.g., Turner et al. 1996; Black et al. 2003; Crk et al. 2009). One comprehensive analysis focused on changing spatial patterns in forest landscapes of the interior Columbia Basin, located in the northwestern US (Black et al. 2003). This study considered a wide range of social and biophysical correlates, including demographic, cultural, climatic, topographic, and geologic factors. The authors hypothesized that patterns of change would be explained by social and biophysical variables operating at a similar scale, but changes were not necessarily correlated to factors at the same scale. Broad-scale social variables, including land ownership, economic market structure, and cultural values, were important covariates in all models. Biophysical parameters related to local growing conditions modified these influences (Black et al. 2003). Results confirmed the strong influence of humans on landscape patterns and identified interactions with biophysical variables that were difficult to predict; in the authors' words, "The story is overwhelmingly that of social system factors imposed on biophysical factors" (Black et al. 2003).

Interacting drivers are also key in wildland landscapes, and recent studies in the Serengeti ecosystem nicely illustrate this point while also demonstrating the use of simulation modeling to study pattern–process interactions. The Serengeti is a well-studied savanna-grassland landscape in east Africa that is especially famous for its native wildlife. The spatial patterns of tree cover in the Serengeti landscape change over time and are difficult to predict. Using a spatial simulation model that included vegetation, fire and dominant herbivore dynamics, Holdo et al. (2009) detected interactions among multiple drivers of pattern. For examples, elephants and fire had synergistic negative effects on woody cover; fire increases the heterogeneity of tree cover when grazers are present, but decreases that heterogeneity when grazers are absent; the steep rainfall gradient in this landscape directly affects the pattern of tree cover in the absence of fire, but with fire, the woody cover is determined by the grazing patterns of migratory wildebeest (Holdo et al. 2009). Thus, as mobile consumers, grazers could greatly affect the spatial patterns of tree cover in the Serengeti via their effects on fire.

Thresholds and Nonlinearities

Another challenge to predicting landscape patterns involves nonlinear dynamics and thresholds. An *ecological threshold* is the point at which there is an abrupt change in an ecosystem quality, property, or phenomenon, or where small changes in an environmental driver produce large responses in the ecosystem (Groffman et al. 2006b). If a landscape is characterized by thresholds that have not been resolved, future changes are likely to be surprising. As we discuss in detail in Chap. 3, the connectivity (or fragmentation) of habitat patterns change nonlinearly with the proportion of the landscape occupied by the habitat.

Social–Ecological Systems

The past decade has seen a tremendous increase in the number of studies trying to integrate social and ecological drivers of landscape patterns and changes in meaningful ways. Given the dominant influence of human activities on global ecosystems, the importance of this is apparent. However, such interdisciplinary studies are difficult, in part because of the need to integrate quantitative and qualitative approaches, and in part because disciplinary traditions can be hard to bridge. Early approaches used quantitative proxies for social drivers, including land ownership, population density, distances to nearest road or market centers (e.g., Spies et al. 1994; Turner et al. 1996; Wear et al. 1996). Contemporary studies attempt to integrate institutions, governance structures, and cultural attitudes (e.g., see Turner and Robbins 2008). Successful studies usually require multi-investigator teams that include natural and social scientists. Furthermore, it remains important to continue development of methods that allow qualitative and quantitative data to be combined for analysis (Bürgi et al. 2004).

Limited Ability to Perform Experiments

Experimentation is often considered the "gold standard" for demonstrating mechanism and causality. In landscape studies, experimentation at broad spatial scales is often logistically impossible, and one is often limited to studying correlations (Bürgi et al. 2004). Hypothesized causalities between drivers and landscape patterns or changes can be evaluated statistically (e.g., Bürgi and Turner 2002; Crk et al. 2009). Another approach borrows from historical methods and reconstructs landscape history in narrative form using methods such as oral histories to augment archival data sources. For example, a case study of landscape history in a Peruvian Amazon landscape from 1948 to 2005 identified key socioeconomic drivers (e.g., boom and bust in demand for barbasco, a native plant that contains rotenone in its roots; commercialization of DDT; introduction of agricultural credit programs) that were related to observed landscape changes (Arce-Nazario 2007). Such place-based studies probe the complexity of landscape dynamics and are rich in detail and understanding, although they may not be general. To understand landscape pattern and change, landscape ecologists generally use a multipronged approach that includes comparative study of landscapes that differ in putative drivers, simulation models in which the consequences of different drivers can be explored, and "natural experiments" that may include disturbances or human land-use patterns.

In conclusion, landscape patterns are generated by complex relationships among multiple factors. Every landscape has resulted from multiple and contingent causation. History both shapes current conditions and constrains future responses, and current landscape patterns are creating legacies for the future. Landscape ecologists need a healthy appreciation for multiple causality, a lengthy temporal perspective, and an awareness of legacies.

SUMMARY

Today's landscapes result from many causes, including variability in abiotic conditions such as climate, landform, and soils; biotic interactions that generate spatial patterning even under homogeneous conditions; past and present patterns of human settlement and land use; and the dynamics of natural disturbance and succession. All landscapes have a history, and determining the conditions that gave rise to different landscapes in the past is critical for anticipating the future. Every landscape is unique because the combined, interacting effects of multiple environmental controls and drivers generate a landscape that is unlikely to be duplicated exactly at any other place or time. Any particular landscape is a singular outcome from a range of plausible outcomes. Historical and spatial contingencies play a big role.

Variability in climate and landform is observed over broad scales, and these abiotic drivers constrain other causes of landscape change. Climate effects are modified by landform—which includes both geology and topography, or physical relief. The distribution of plant and animal communities and indeed of entire biomes has varied tremendously with past changes in climate, even in the absence of human activities. Not only have species varied in their ranges, but also the local abundances—and thus relative dominance—of taxa have changed. Landforms are important influences on landscape pattern because they influence moisture, nutrients, and materials at sites within a landscape; they affect flows of many quantities; they may influence the disturbance regime; and they constrain the pattern and rate of geomorphic processes. Landscape ecologists must understand the influence of climate and landform on the biota and recognize the dynamic responses of the biota to variability in climate in space and time.

Interactions among organisms, such as competition, facilitation, and predation, may lead to spatial structure, even in the absence of abiotic variation. Keystone species or dominant organisms may define spatial pattern on a landscape. Disturbance and succession are key contributors to landscape pattern. Humans are also a strong driver of landscape patterns, as land-use patterns interact with the abiotic template to create the environment in which organisms must live, reproduce, and disperse. Nearly all landscapes, even those we perceive as "natural" today, probably have a history of human influence that dates back a long time. Many landscapes today have become mosaics of natural and human-influenced patches, and once-continuous natural habitats have become increasingly influenced by human activities. Effects of past land use (i.e., land-use legacies) are increasingly recognized as important determinants of the present-day biota that inhabit our landscapes. Studies in Europe have demonstrated legacies of land use that have persisted for over 1000 years. The future legacies of contemporary land-use patterns may shape landscapes for decades and centuries to come. Explaining and predicting landscape change remains challenging because of multiple interacting drivers, thresholds and nonlinearities, complex interactions with social drivers, and the limited ability to experiment at landscape scales.

DISCUSSION QUESTIONS

1. What is meant by the concept of the "perfect landscape," and how does this concept influence the way we explain contemporary landscape patterns or project future patterns?
2. Consider the variety of factors that create landscape pattern. How would you rank their relative importance? Do you think this ranking has changed through time? Explain your answers.
3. Why is it important to understand the history of a landscape? What types of effects of events from the past may remain in a present-day landscape patterns?
4. As human influences intensify and climate change continues, how do you think landscape ecology should evolve so that it can help address key questions of the twenty-first century?

FURTHER READING

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CHAPTER

3

INTRODUCTION TO MODELS

Models are essential tools in landscape ecology, as they are in many scientific disciplines. Spatial models, in particular, play a prominent role in evaluating the consequences of landscape heterogeneity for ecological dynamics. Because we refer to models throughout this book—and because we are aware that many students have had little training in modeling or systems ecology—the first part of this chapter presents an elementary set of concepts, terms, and caveats for students to understand what models are, why they are used, and how models are constructed and evaluated. We also define what we mean by a spatial model and indicate the circumstances where spatial models will be most useful. The second part of this chapter introduces neutral landscape models (NLMs) and illustrates the utility of simple models for understanding landscape heterogeneity and testing hypotheses linking pattern with process. There are many excellent texts that address modeling issues in greater depth. Students interested in the modeling process are referred to the recommended readings at the end of the chapter.

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WHAT ARE MODELS AND WHY DO WE USE THEM?

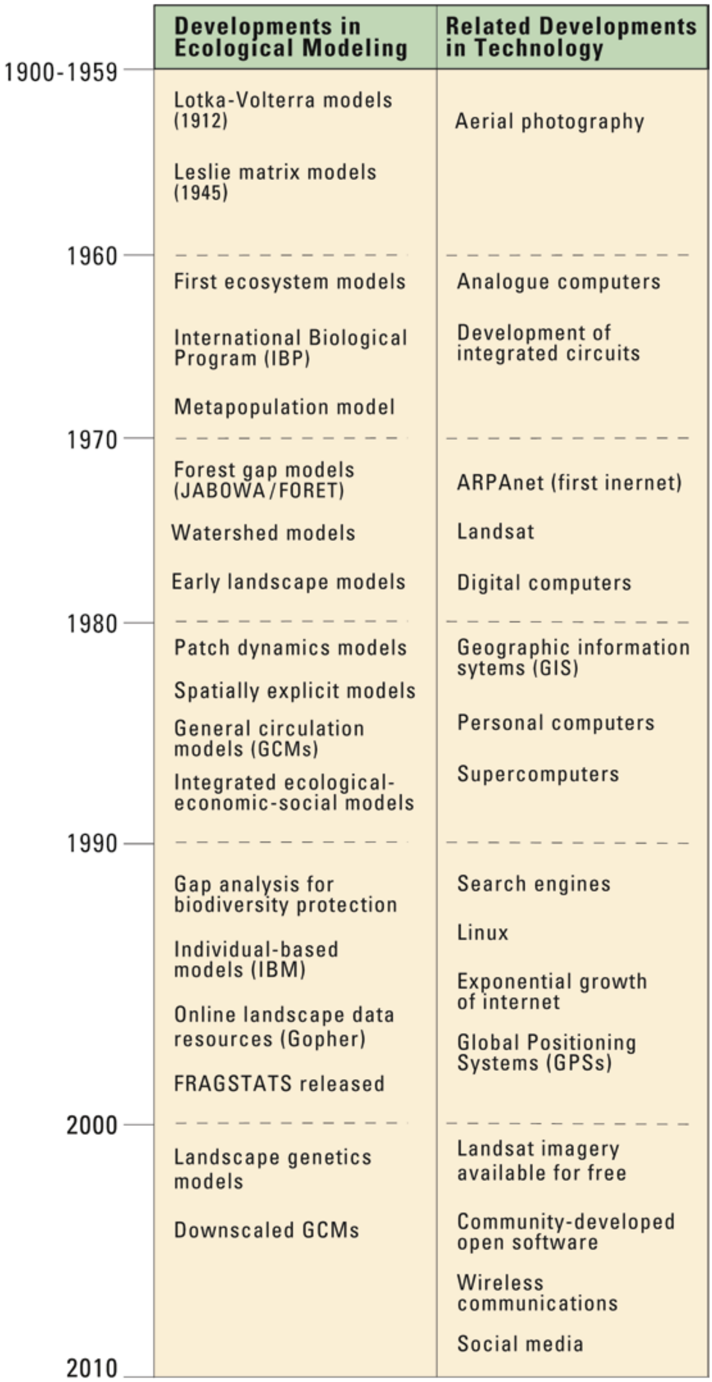
What Is a Model?

A model is an abstract representation of a system or process. Models can be formulated in many different ways. Physical models are material replicas of the object or system under study, but at a reduced size; for example, models of ships and airplanes are developed to better understand the forces that act upon them, and architectural models allow the space and structure of a building to be visualized. Physical models are used in many branches of engineering, but ecologists also build physical models of streams, ponds, and even whole ecosystems (Perez et al. 1991; Macilwain 1996; Petersen et al. 2003) providing an important bridge between experiments in natural systems and theoretical models (Stewart et al. 2013). In contrast, abstract models use symbols rather than physical devices to represent the system being studied. For example, verbal models are constructed out of words, graphical models are pictorial representations, and mathematical models use symbolic notation to define relationships describing the system of interest. We focus here primarily on mathematical models, which have played an important role in ecology since the beginning of the twentieth century (Fig. 3.1).

Why Landscape Ecologists Need Models

George E. P. Box (1979) stated in this oft-repeated quote, “All models are wrong, but some are useful.” Models are useful because they allow us to precisely define the problem, articulate the relevant concepts, and then provide a means of analyzing data and communicating results. Most importantly, models allow us to predict the logical outcomes of how we think a system works and then explore the suite of conditions that vary in time and space. Because knowledge is always incomplete, and all data needed to build a model are never available, all models require assumptions to “fill in the blanks.” Therefore, most models are used to explore the consequences of our assumptions and hypotheses rather than to represent system structure and dynamics definitively. Models should always be regarded as one of the scientific tools for achieving a specific end rather than as goals unto themselves.

When ecologists are faced with answering questions in a large and complex landscape, it is difficult—sometimes impossible—to sample every possible combination of conditions or to conduct experiments at the ideal spatial and temporal scales. The cost of landscape experiments in time and money is often prohibitive. Some management options have been evaluated using experimental methods (see Bowers et al. 1996; Mabry and Barrett 2002; Haddad et al. 2003; Joshi et al. 2006) while manipulations of microlandscapes have provided valuable insights into the



	Developments in Ecological Modeling	Related Developments in Technology
1900-1959	Lotka-Volterra models (1912) Leslie matrix models (1945)	Aerial photography
1960	First ecosystem models International Biological Program (IBP) Metapopulation model	Analogue computers Development of integrated circuits
1970	Forest gap models (JABOWA/FORET) Watershed models Early landscape models	ARPAnet (first inernet) Landsat Digital computers
1980	Patch dynamics models Spatially explicit models General circulation models (GCMs) Integrated ecological-economic-social models	Geographic information sytems (GIS) Personal computers Supercomputers
1990	Gap analysis for biodiversity protection Individual-based models (IBM) Online landscape data resources (Gopher) FRAGSTATS released	Search engines Linux Exponential growth of internet Global Positioning Systems (GPSs)
2000	Landscape genetics models Downscaled GCMs	Landsat imagery available for free Community-developed open software Wireless communications Social media
2010		

Figure 3.1.

Timeline of the development of models in ecology, with important technological and programmatic developments that influenced ecological modeling highlighted. Developments shown are not comprehensive but selected for illustration.

response of insects, small mammals, and some plants to alternative patterns (e.g., Johnson et al. 1992; Glenn and Collins 1993; Imes et al. 1993; Wiens 1995; Wiens et al. 1995; With et al. 1999; Brinkerhoff et al. 2005; Johnson and Haddad 2011). However, extrapolation of these results to large regions remains a perplexing problem (see Chap. 1). Landscape ecologists more commonly use field studies to provide correlative relationships—for example by comparing locations that vary in their degree of land-cover or connectivity of a specific habitat type. Natural disturbances have also been used as "uncontrolled experiments" with their effects expressed in quantitative terms (see Chap. 6). However, all these approaches are limited in the range of conditions, replication, or control. Under these circumstances, the unique features of each landscape or disturbance event may dominate results. Models can be used to relax empirical constraints, providing a means of systematic comparison across a broad range of conditions, but they do so at the cost of increased levels of unknowns and uncertainties.

It has been more than 20 years since Baker (1989a) and Sklar and Costanza (1990) first reviewed landscape models. Focused reviews on specific topics have been published since then (e.g., Turner et al. 1994b; Lambin 1997; Fries et al. 1998; Perry et al. 2004a; Perry and Enright 2006; Keane et al. 2007; Scheller and Mladenoff 2007), but the ambitious task of assembling a comprehensive overview of the broad range of topics and applications found in landscape ecology has not been attempted. An informal survey of papers listed in ISI's Web-of-Science (2011) over the last 10 years (2001–2011) referencing both "landscapes" and "model" for a subset of journals (AMERICAN NATURALIST, BIOLOGICAL CONSERVATION, CONSERVATION BIOLOGY, ECOLOGY, ECOLOGICAL APPLICATIONS, ECOLOGICAL MODELLING, LANDSCAPE ECOLOGY, and OIKOS) showed that over 1167 papers have been published within this topic area in the last 10 years. These papers represent a wide diversity of topics and approaches and illustrate the difficulty of placing landscape models into simple, discrete categories necessary for a coherent review. The volume and diversity of approaches are healthy signs of the continued growth of this field of research, but both also make a judicious choice of modeling approach even more challenging. A clear and simple paradigm for addressing this issue has yet to emerge. Consequently, useful modeling strategies and examples for studying pattern and process in changing landscapes will be presented throughout the remainder of this book.

Models may be used to formalize understanding, define unknowns, guide field studies, develop theory, or make predictions. All these objectives will require a careful strategic and tactical approach. *Strategic issues* are those concerned with setting objectives and selecting an approach that minimizes errors; *tactical issues* are those concerned with the details of model construction, testing, and application.

STRATEGY FOR DEVELOPING MODELS

All models are simplifications of real systems (Risch et al. 2005; Hunt et al. 2007). Therefore, the first strategic issue is to define the purpose and scope for the model, the inherent limits of available information and measurements, and to consider the consequences of model error on results.

Define the Problem and Develop a Conceptual Model

A specific statement of model objectives provides the framework for model development and the context within which simulation results must be interpreted. Definition of the problem should be as specific as possible, allowing one to determine the form of the model, the degree of complexity needed, and the spatial and temporal scales at which it will operate (Grant et al. 1997). Once the problem is stated, a conceptual or qualitative model can be developed. The conceptual model identifies system boundaries (the temporal and spatial scales and associated inputs and outputs), the model components (state variables), and the relationships among the state variables. A conceptual model of sufficient detail allows the important variables and parameters (coefficients that control model processes), the system drivers (driving variables, see Table 3.3 in Appendix) and the required inputs and outputs to be defined. The appropriate level of spatial and temporal resolution for the model (i.e., model scale) is a key consideration in a conceptual model (Fig. 3.2). Once formally stated, the model developer should consider the following three issues that affect the adequacy of the approach defined by the conceptual model.

Trade-offs Among Generality, Precision and Realism

Levins (1966) stated that no model can be completely realistic, always precise, and generally applicable (but see Orzack and Sober 1993). Levins's provocative paper stated: "It is… desirable to work with manageable models which maximize generality, realism, and precision [in order to reach the goals] of understanding, predicting, and modifying nature" (Fig. 3.3). Consequently, a strategic approach to model development is one that is cognizant of these trade-offs. Levins used familiar models of population biology to illustrate this problem. We review Levins' list here, providing parallel examples from the recent literature of landscape modeling.

Sacrifice generality to realism and precision. Most models that trade generality for realism and precision produce place-based results. By specifying particular cases (or scenarios), a reduced parameter space may be defined and relevant measurements made. Models that emphasize realism and precision are often closely calibrated so that they closely mimic observed dynamics of the focal landscape.

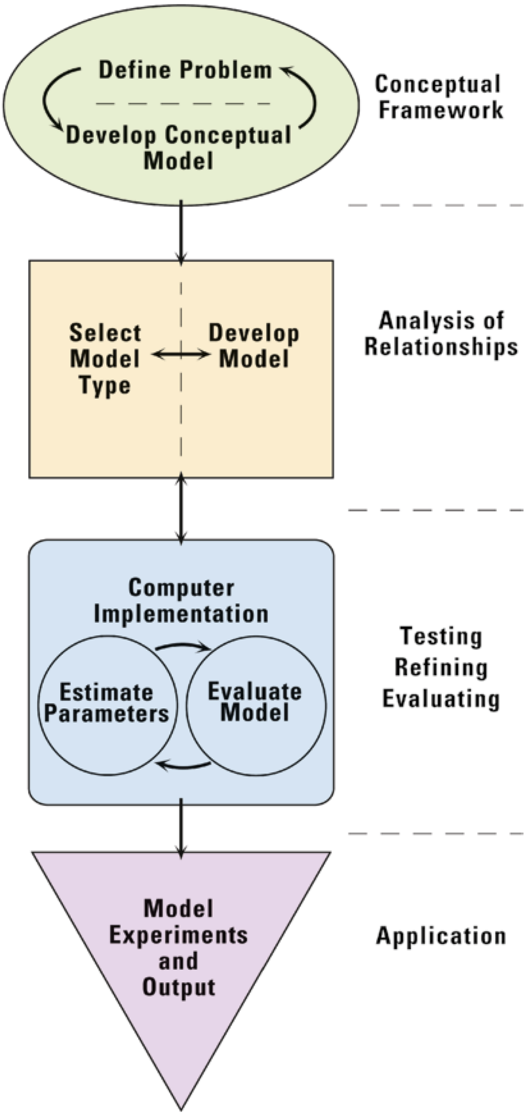


FIGURE 3.2.
Flowchart illustrating the major steps in building a model.

Results may be tested (i.e., confirmed or rejected), but general conclusions across a broad spectrum of landscapes will be limited. Examples of this approach include landscape models that focus on specific locations where precisely measured parameters may be obtained (e.g., Jantz et al. 2004; Ferrari et al. 2009). Iterative application across a suite of conditions (e.g., Scheller et al. 2007; Sturtevant et al. 2009) may be used to introduce stochastic effects and increase generality.

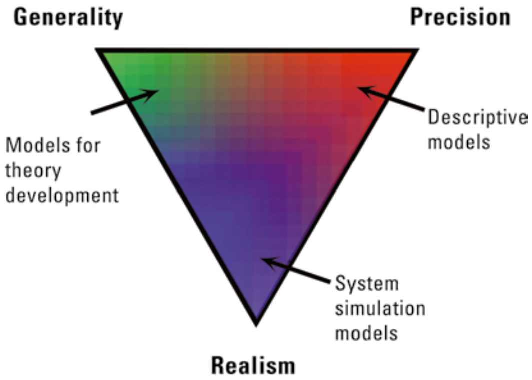


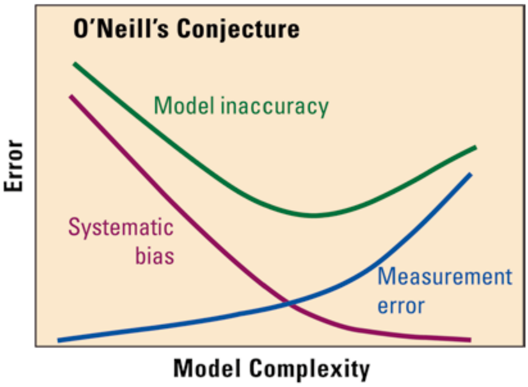
FIGURE 3.3.
Schematic representation of Levins (1966) conceptualization of the trade-offs between a model's generality, precision and realism usually encountered in the development and use of ecological models.

Sacrifice realism to generality and precision. Landscape models often adopt this trade-off and strive for a correct average result rather than a specific prediction of what will happen at a particular time or place on a given landscape. Such models ignore highly detailed interactions and usually employ equations with a reduced parameter set. If the details excluded from the model have a minor effect on the results, or the sum of all ignored details cancel out, then a simple model may be more general and more precise. Examples of this approach include models that propagate disturbance over large areas and long time periods (e.g., Gardner et al. 1999; Keane et al. 2007). Models predicting equilibrium conditions may also sacrifice reality for generality (e.g., Chave and Norden 2007), using this theoretical endpoint as a measure of the effect of changing processes. The simple NLMs presented later in this chapter also exemplify this trade-off.

Sacrifice precision to realism and generality. This trade-off is often adopted when the desired result is qualitative rather than quantitative. Many theoretical models fall into this category, and they make very general predictions that are not directly applicable to a particular place or set of measurements. Examples include GAP models (Scott et al. 1993; Kiester et al. 1996), island biogeography, and neutral theory (Hubbell 2001) and extinction debt (Tilman et al. 1994).

It is the general consensus that Levins' trade-offs are general and may not be easily avoided. The form of the model and quality and quantity of available data define the domain over which model results may be reliably used for understanding, prediction, and/or management. The comparison of alternative models that differ in their assumptions and simplifications (see Gardner et al. 1999; Keane et al. 2007; Yang et al. 2008 for examples from the fire literature) are the best means for checking the limits and broadening the scope of conclusions drawn from a single model (Levins 1966).

FIGURE 3.4.
A conceptual representation of the conjecture by O'Neill (1973) that simple models may have significant errors due to absence of important processes (*red line*) while complex models have error associated with unmeasured (or unmeasurable) parameters and processes (*blue line*). The conjecture is that there is an optimum level of model complexity that minimizes total error (*green line*).



TRADE-OFFS BETWEEN MODEL COMPLEXITY AND MODEL ERROR

It has often been assumed that complex models are more accurate and simple models are more general because simple models may lack essential details, causing systematic bias in predictions—but adding detail to a model does not guarantee an increase in reliability unless the added processes are essential, well understood, and reliably estimated. The potential trade-off between complexity and error was first discussed by O'Neill (1973) who speculated that for any given problem and level of knowledge there may be an optimal level of model complexity (Fig. 3.4). Strayer et al. (2003a) also present a thoughtful discussion of the level of detail to include in models of heterogeneous systems.

Landscape models are often developed with the implicit assumption that the results will only be useful if they are completely realistic (i.e., highly detailed). Because landscapes are diverse and complex, a fully realistic model will be complex with significant data requirements for estimating all model parameters. A counter-strategy for reducing complexity while also improving model reliability is nearly always necessary (Beven 2002). The development of hierarchy theory (Allen and Starr 1982; O'Neill 1989) has shown that the aggregation of similar components into a single unit (i.e., numerous species into fewer functional types; Lavorel and Garnier 2002) reduces the number of parameters that must be estimated and may, therefore, substantially improve results. One may also take advantage of "the law of averages" by setting the realistic temporal and spatial scales for model resolution: If final results can be expressed in hectares and years, then the average values of fine-grained values (e.g., hours to days, meters to hectares) can be used to produce more precise results (Peters et al. 2004a).

In all cases, it is important to evaluate model error. The first step should be to compare model output with available data graphically, testing whether results fall within the confidence limits of empirical results. These comparisons should specifically focus on the model objectives: If the purpose of the model was to assess the direction of change (i.e., an increase in urbanization) then only the direction of change needs to be assessed; if the purpose was to locate areas where change has occurred (a more difficult task), then spatial statistics may be required to verify model response. The strategic issue is that model-data comparisons are most meaningful when objectives have been clearly and precisely defined. More formal methods of sensitivity and error analysis (Gardner et al. 1981; Jager and King 2004) are useful for identifying model components and parameters that most contribute to model errors.

When Should Models Be Spatially Explicit?

Most generally, a model should be spatially explicit when the inputs, the outputs, or the processes required by the modeling objectives and conceptual formulation vary spatially (Strayer et al. 2003a). If spatial pattern is a driving variable—that is, the model needs to predict the consequences of alternative configurations of *input* conditions or forcing variables—then a spatially explicit model is warranted. Examples include models of the effect of habitat arrangement (not simply amount) on population dynamics; the effect of arrangements of riparian buffer habitats on nutrient loading to surface waters; of the effects of alternative distributions of resources on the movement or foraging patterns of animals; and the positive (or negative) effects of pathways or corridors for animal dispersal (Lookingbill et al. 2010; Sullivan et al. 2011). A spatially explicit model is also warranted if predicting changes in spatial pattern is required—that is, the model *output* must be spatial. Examples include models that predict the distribution and abundance of animals in a landscape at a future point in time; future spatial patterns of habitat in response to animal movements and foraging patterns; and land-cover patterns that respond to alternative land-use activities or management strategies. Lastly, a spatial model is needed when the *processes* themselves interact within a local neighborhood to generate patterns, such as when competition between neighboring organisms generates distribution patterns, or when the process itself has a spatially explicit response, such as the actual flow path of water or nutrients, or the actual migration or dispersal pathway of an organism (Fig. 3.5). Thus, the model goals determine whether a spatial model is needed.

A fully spatially explicit model will have explicit spatial locations for all variables and inputs. Nonspatial or spatially implicit models may produce maps as output, making these approaches appear to be spatially explicit when, in fact, they are not. For instance, maps produced by a table look-up process (e.g., nutrient dynamics; Burke et al. 1991; 1999) do not consider location-specific effects and, hence, are spatially implicit predictions. The complexity required to develop and test a spatially explicit model is significantly greater than a spatially implicit model, making spatially explicit approaches only desirable when local effects are known to dominate results measured at landscape scales (Peters et al. 2004a).

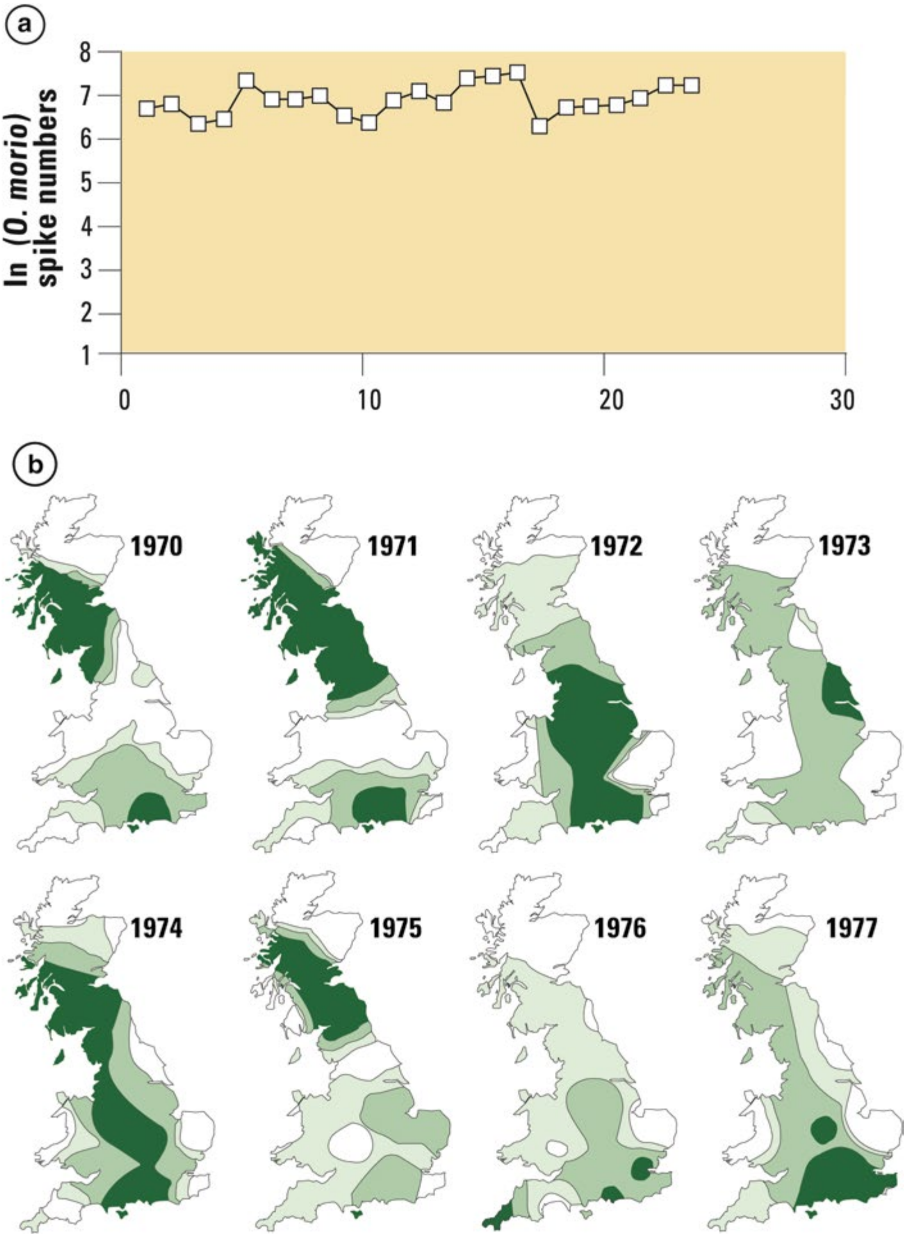


FIGURE 3.5.

Comparison of temporal vs. temporal + spatial population dynamics. (**a**) Shows the change through time in a population of the green-winged orchid, *Orchis morio*, at one locality. In this case, changes are temporal only. (**b**) Shows the change in the spatial distribution in Great Britain of elder aphid (*Aphis sambuci*) between 1970 and 1977, where the density of the shading represents local population density. This illustrates changes through both space and time; predicting such dynamics would require a spatial model.

ADAPTED FROM GILLMAN AND HAILS (1997.)

To summarize the strategic issues: One should apply the law of parsimony when developing a model by precisely defining the models purpose, developing the simplest conceptual model possible, adding complexity only when it is necessary and supported by data, use a hierarchical approach to define model variables and processes; and planning on revisiting these strategic steps when model errors indicate the need for improvement.

TACTICS FOR MAKING THE MODEL WORK

The tactical steps for developing a working model are derived from the systems ecology approach to ecological modeling (Fig. 3.2) developed primarily by engineers for characterizing the dynamics of complex physical systems. The success of the systems approach had a strong influence in the early development of landscape ecology in both Europe (Opdam and Schotman 1987; Naveh and Lieberman 1990; Zonneveld 1995) and North America (Johnson et al. 1981; Gardner et al. 1987; Opdam 1987; Sklar and Costanza 1990) and continues to be the dominant paradigm for model development today (Wu and David 2002; Costanza and Voinov 2004; Lookingbill et al. 2008). The basic principles of the systems approach go back to the philosophy of holism formulated by Smuts (1926) and developed more rigorously by Von Bertalanffy (1968, 1969). Numerous works written more than 30 years ago describing the principles of general systems theory and their application to ecological systems are still relevant today (e.g., Watt 1968; Van Dyne 1969; Patten 1971). Here, we draw from the sequence of modeling steps outlined in Kitching's (1983) text on systems ecology. We also provide a reference table for terms commonly used in modeling (see Appendix, Table 3.3). Readers may wish to refer to Swartzman and Kaluzny (1987) and Haefner (2005) for excellent introductions to the tasks associated with model development.

Once the conceptual model has been developed, a wide variety of mathematical formulations may be used to transform the "concept" into an operational model. A wealth of model types has been used in landscape ecology (as discussed throughout the book), but it is beyond our scope to review and describe these techniques here.

The programming language or simulation software for implementing a model is usually selected based on local resources, experience and expertise. Often, a decision must be made between whether to program a new model or to use an existing model. For example, a number of existing models, such as the forest landscape simulator LANDIS (Mladenoff and He 1999; Sturtevant et al. 2009) and the ecosystem model Century (Parton et al. 1992; Gilmanov et al. 1997), have been used widely. The use of an existing model eliminates the need for massive amounts of programming and analysis, but the existing structure (and the developer's strategic decisions that led to this structure) may constrain the questions that a new user desires to ask. Furthermore, it is difficult for new users to become deeply familiar with the workings of complex models. Regardless of the software decision, all model implementations require systematic checking for the adequacy of relationships represented and the accuracy of methods employed. This phase, often referred to as *model verification*, may require more time and energy than any other step represented in Fig. 3.2. An important adjunct to this stage is the production of adequate *model documentation* and the ultimate public availability of the final source code.

The specification of values for the model parameters, model inputs, and initial values of the state variables within the model (see Appendix, Table 3.3) are typically estimated from data or obtained from published values. The process of parameter estimation differs from model *calibration*—the iterative adjustment of parameters to improve model fit to measured output variables. Calibration may be required when direct estimates of parameters are not available but net changes in system dynamics have been measured, providing the objective criteria for parameter adjustments. The errors associated with calibrated values are unknown unless a second data set is available to test the adequacy of calibrated (but unmeasured) parameters.

Once operational, a model must be evaluated for its utility. Does model behavior agree with empirical observations? Are the underlying assumptions reasonable? Do those assumptions result in realistic behavior? Objective comparison of model results with data, sometimes referred to as *model validation* (Rykiel 1996) provides the necessary confidence in predictions to make models useful and define the conditions over which the model will be most reliable. Although the term "validation" continues to be widely used (e.g., Scheller and Mladenoff 2004; Nuttle and Haefner 2007), because this term connotes "truthfulness," its unqualified use can be confusing and is generally discouraged (see Mankin et al. 1975 for a thoughtful discussion of validation issues).

When the steps illustrated in Fig. 3.2 have been completed, the ecologist has a tool that may be used to conduct experiments and predict outcomes. The verification of predictions across a range of conditions confirms or rejects the model hypotheses and assumptions, providing new insights into system behavior. As confidence builds, model applications may move from hypothesis testing to more serious applications such as conservation planning and planning. Care must be taken at each stage of model development to assure the accuracy and adequacy of the model. In spite of the availability of software that eases the process of model development, there is always the danger that insufficient attention to each step of development will produce unreliable results. Because no amount of care will guarantee that a model is a perfect representation of the ecological system it was intended to mimic, the comparison of results with alternative models (Levins 1966) continues to be sage advice for the careful scientist (Box 3.1).

Box 3.1
CAVEATS IN THE USE OF MODELS

Wise application of modeling tools recognizes the pitfalls and problems of model development and interpretation. We review here, in concise form, what we consider to be the most important caveats for modeling in landscape ecology:

1. *Know thy model*. The performance of each model is the logical consequence of the hypotheses and assumptions upon which that model is based. Alternative assumptions regarding systems behavior might be equally viable, but produce dramatically different results. Comparison among alternative model formulations is extremely desirable, and should be attempted where possible (see Kittel et al. 1996; Pan et al. 1998; Miranda et al. 2009 for examples).
2. *Errors propagate*. Small errors in sensitive parameters can lead to large errors in outputs (Rose et al. 1991). Techniques for the analysis of effects of parameter errors are available (Metzgar et al. 1998) and should always be employed before predictions are made. Assessment of errors of spatially explicit models remains a challenge (Khan et al. 2006; Minor et al. 2008), largely because of the added complexity of evaluating qualitative and quantitative spatial predictions.
3. *All models are simplifications of reality*. This is not a casual philosophical statement! It simply means that no single model will ever be a completely adequate description of reality. Therefore, the goal of model studies should be to define the applications for which a given model provides reliable and useful results. New applications of old models are not released from this requirement.
4. *There are never enough data*. The incomplete nature of data often requires parameter values to be estimated from a diversity of sources. Inconsistency in the methods of data collection and parameter estimation may result in model biases that are difficult to identify. Gaps in empirical information that do not allow adequate estimation of key parameters are often the greatest source of uncertainty in model predictions.
5. *High tech methods do not guarantee a "good" model*. Technologically advanced methodologies, including the availability of higher level programming languages that facilitate model coding, do not assure the accuracy or reliability of results. When developing or interpreting models, it is critical for the user to understand fully the structure of the model, the assumptions that went into its development and the constraints (such as spatial or temporal scales) on its appropriate use.
6. *Keep an open mind*. There is no single paradigm for spatial modeling of landscapes. Model development and testing requires a broad perspective of landscape ecology and systems analysis techniques.

NEUTRAL LANDSCAPE MODELS

As development of landscape ecology accelerated and spatial heterogeneity received increased attention, new models that could represent explicit spatial patterns and allow different aspects of pattern to be varied were needed. Also needed was a yardstick against which the potential influence of different spatial patterns could be evaluated. NLMs were developed in the late 1980s to fill this gap (Gardner et al. 1987).

Neutral Models in Ecology

The sequential development and testing of hypotheses is essential for progress in science (Platt 1964; Quinn and Dunham 1983). The simplest hypothesis that one should first construct is the null hypothesis of no effect (Fisher 1935)—i.e., landscape processes are not responsible for the observed pattern. A properly formed null hypothesis provides the required reference point against which alternatives may be contrasted. Because landscape analysis involves relating ecological patterns to complex histories of natural forces and events (e.g., climate, terrain, soils, water availability, biota, natural disturbances, etc.) as well as the consequences of human alterations (e.g., urbanization, agriculture, forestry management, etc.; see Chap. 2), the specification of appropriate null hypotheses is a challenge. Consequently, observational and correlational approaches tend to dominate over the experimentation and hypothesis testing more typical of sciences studying simpler systems (see Strong 1980 for further discussion). The difficulty with corroborative studies is that the uniqueness of each landscape (Phillips 2007) limits the use of experimental designs and the possibility of replicate measures. When treatment effects (i.e., processes dependent change in landscapes) are tested without true replication, the validity of these comparisons is often suspect (Hurlbert 1984; Hargrove and Pickering 1992).

Neutral models, which simulate dynamics *in the absence of specific processes*, have been widely used in ecology for testing the corresponding null hypothesis of statistics (the terms “null” and “neutral” are distinguished here, but are often used interchangeably). For instance, Cole (1951, 1954) used random numbers to construct cycles similar to those observed in natural populations; Simberloff (1974) used island biogeographic theory to examine community patterns; Istock and Scheiner (1987) used random landscapes to test patterns of species diversity; and Nitecki and Hoffman (1987) produced an edited volume on the subject. Other examples include niche shifts in *Anolis* communities (Haefner 1988a, b); community formation in fishes (Jackson et al. 1992); plant migration rates (Higgins and Richardson 1999); hemlock regeneration and deer browsing (Mladenoff and Stearns 1993); bird assemblages in fragmented landscapes (Sisk et al. 1997); tests of Holling’s hypothesis of discontinuities in landscape pattern causing clumps and gaps in the distribution of body sizes within animal communities (Siemann and Brown 1999); and the continued investigations of the formation of structure in natural communities (Wilson 1995). Perhaps the most notable use of neutral models has been Hubble’s provocative theory of biodiversity (Hubbell 2001, 2006) which continues to be widely discussed in ecology (e.g., Lowe and McPeek 2014; Warren 2012).

Neutral Models in Landscape Ecology

A simple standard for landscape pattern—and thus the basis for testing differences between landscapes—is a random map (Fig. 3.6) which lacks all factors that might organize or structure pattern (Gardner et al. 1987; Gardner and Urban 2007). Tests of observed landscapes against replicate random maps reveal the magnitude and significance of differences due to the structure of actual landscapes. Therefore, random maps are *neutral landscape models* (*NLM*) against which effects of processes that structure actual landscapes may be tested. Studies of NLMs have shown that surprisingly rich patterns can be generated by random processes alone—and their use has shown that actual landscapes may not always be measurably different from these random patterns (Gardner et al. 1993; Li et al. 2004).

With and King (1997) reviewed the use of NLMs and separated their uses into two categories: (1) to determine the extent to which structural properties of landscapes (e.g., patch size and shape, amount of edge, connectivity, autocorrelation) deviate from some theoretical spatial distribution, and (2) to predict how ecological processes, such as animal movement, seed dispersal, gene flow, or fire spread, are affected by landscape pattern. A third important use has also emerged: to evaluate new methods of numerical analysis, including the development and testing of landscape metrics (Li et al. 2005; Gardner and Urban 2007; Wang and Malanson 2007). We next provide a brief overview of the methods behind the generation of random maps and uses in landscape studies.

Random Maps: The Simplest Neutral Model

The simplest method of generating a map is to randomly locate sites within a 2-dimensional grid. This may be efficiently accomplished by using a uniform random number generator (URN) found within most computer languages and mathematical software tools. The URN function typically produces numbers that vary randomly over the interval of 0.0–1.0. The generation of a random map with a single land-cover type is accomplished in two steps: (1) An array of m columns and n rows with $m \cdot n$ elements (sites) is constructed; (2) For each map site a single URN is generated: If the URN is less than a prespecified probability value, p, the site is set to 1; if not, the site is set to 0. For instance, if $p = 0.4$ the grid site will be set to 1 if URN ≤ 0.4, or to 0 if the URN is >0.4. For maps of sufficient size (m and n each >250) the proportion of sites set to 1 will be very close to the value of p while the number of sites set to 0 will be approximately $1 - p$ (e.g., $1.0 - 0.4 = 0.6$). The total number of matrix elements (i.e., grid sites or cells) occupied by the habitat (land-cover) type of interest will be approximately equal to $p \cdot m \cdot n$ while the number of sites of "nonhabitat" will equal $(1 - p) \cdot m \cdot n$.

As the grid is filled with 0's and 1's, *clusters*, or *patches*, of the land-cover type will form (Fig. 3.6). Clusters are identified with rules defining contiguous sites. The simplest rule defines clusters as groups of sites of the same land-cover type with at

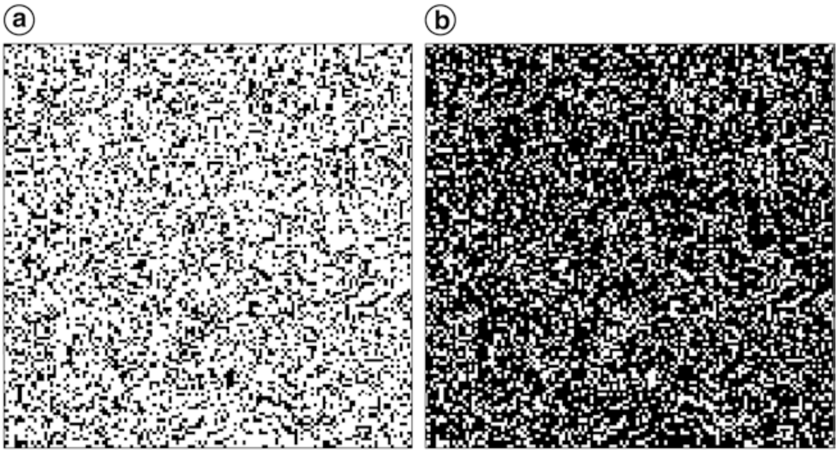


FIGURE 3.6.
A random map (m, the number of rows and columns equals 64) generated with the probability, p, that grid cells contain the land-cover type of interest. The black cells represent (**a**) 0.3 and (**b**) 0.7 of the landscape. The user may determine, by hand, that the largest cluster of the black cover type percolates in (**b**).

least one horizontal or vertical (but not diagonal) edge in common. This rule for cluster (patch) identification is usually referred to as the "four-neighbor" or "nearest-neighbor" rule, and it is a conservative estimate of habitat adjacency (also see discussion in Chap. 4 and Fig. 4.9). When a series of maps is generated with increasing values of p, the number of patches increases over the interval $0.0 < p < 0.3$; as p continues to increase small patches coalesce into larger ones and the total number of patches declines (Gardner et al. 1987; Gardner 2011; Fig. 3.7a). The amount of edge on the map is also affected by p, with the maximum amount of edge occurring when $p = 0.5$ (Gardner et al. 1987; Fig. 3.7b).

The total extent of the map (i.e., the value of m and n representing the number of rows and columns, respectively) also affects measures of pattern. Smaller maps (i.e., lower values of m and n) will cause patches to be truncated by the map boundary. This effect is most noticeable when p is >0.6 (Gardner et al. 1987). Table 3.1 illustrates the truncation effect for a variety of map types and sizes ($m = n = 64$, 128, 256). For random maps with $p < 0.5$ the size of clusters in smaller maps is approximately 80 % of the size of clusters in the larger maps—indicating that truncation effects due to map size result in systematic underestimation of patch size. The truncation effect becomes more noticeable as the value of p increases. At $p = 0.5$ clusters are approximately 70 % that of the next largest map size; and at $p = 0.7$ and 0.9 (Table 3.2) cluster sizes of the smaller maps are approximately 25 % the size of the next largest map!

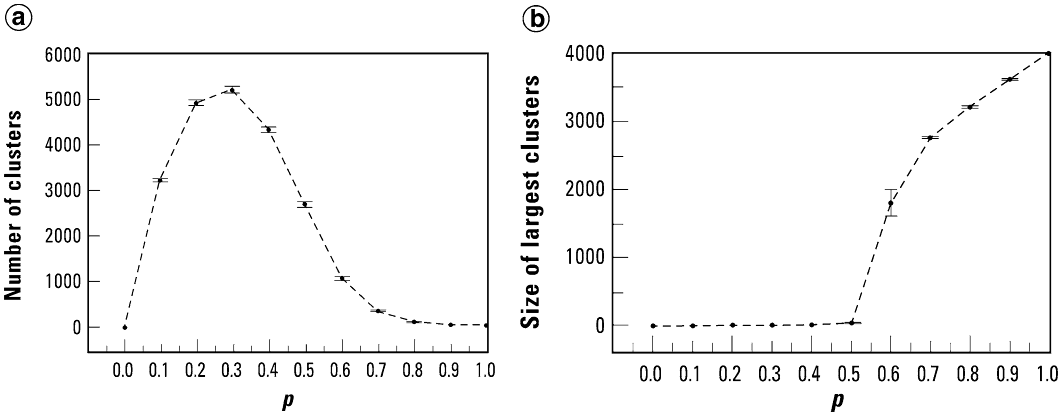


FIGURE 3.7.

(**a**) The number of clusters and (**b**) size the largest cluster for random maps that vary in the probability, *p*, that a grid cell contains the habitat type of interest. Plotted from data reported in Tables 1 and 2 of Gardner et al. (1987) for maps with 200 rows and columns.

TABLE 3.1.

PERCOLATION THRESHOLDS FOR 2-DIMENSIONAL MAPS WITH DIFFERENT NEIGHBORHOOD RULES.

Lattice geometry	Neighboring sites	p_c
Square	4	0.59275
	8	0.40725
	12	0.292
	24	0.168
	40	0.098
	60	0.066
Triangular	6	0.5
	12	0.295
	18	0.225
Honeycomb	3	0.6962
	12	0.3

TABLE ADAPTED FROM PLOTNICK AND GARDNER (1993)

Table 3.2.
Average number of sites composing a cluster (i.e., patch size in grid cell units) as a function of map size (number of rows and columns) and p, the fraction of sites occupied.

Map size	Map type^a	p				
		0.1	0.3	0.5	0.7	0.9
64×64	Random	5.2	21.4	167.0	2780	3680
	$H = 0.2$	124	574	1360.0	2620	3660
	$H = 0.8$	216	908	1760.0	2760	3670
128×128	Random	6.3	27.4	255.0	11,200	14,700
	$H = 0.2$	482	2140	5600	10,500	14,600
	$H = 0.8$	1110	3720	7160	11,100	14,700
256×256	Random	7.6	33.4	350	44,900	58,900
	$H = 0.2$	1760	9190	21,800	42,200	5860
	$H = 0.8$	4450	15,000	28,400	44,300	58,800

Averages based on 100 independently generated maps (Maps were generated and analyzed using RULE (Gardner 1999). Although the documentation of RULE is recent, this is the same program originally used to generate neutral models (Gardner et al. 1987)).

[a] Map types are: Random = simple random map; $H = 0.2$, a multifractal map with the value of H of 0.2; $H = 0.8$, a multifractal map with the value of $H = 0.8$. See text for discussion of multifractal maps.

Why does the truncation effect depend on the value of p? Are there general rules of pattern formation in simple random maps that provide insight into the analysis of landscape patterns? It is these types of question that have been a primary focus of percolation theory (Stauffer and Aharony 1992) from which the first NLM were derived (Gardner et al. 1987). A central concept to emerge from percolation theory was the strong dependency of pattern on the choice of value for p and the existence of a *critical threshold* where small changes in p would result in sudden changes in pattern. The existence of a critical threshold (symbolically defined as p_c) equals 0.59275 when maps are sufficiently large and clusters are defined by the nearest-neighbor rule (Table 3.1). The reason for this threshold is that above p_c occupied sites are so abundant that nearly all sites contact neighbors along one of their four edges causing a single cluster to extend, or "percolate," from one edge of the map to the other. In our previous example (Table 3.2), maps with values of $p > 0.59275$ *will always* result in truncation of the largest cluster on the map. If $p > p_c$ the percolating cluster will continue to increase in size as map dimensions increase. This truncation effect leads percolation theorists to develop the concept of the *infinite cluster*—a cluster that will continue to grow as map dimensions are increased. Thus, there is no finite map dimensions that will fully contain the cluster when $p > p_c$. Although no landscape will have infinite bounds, the practical implication of the "infinite cluster" is that a map 1/2 the size of another will have an average cluster size that is only 1/4 as large.

The general dependence of cluster size on p, and the existence of a critical threshold where small changes in p produce sudden changes in cluster sizes, has important implications for both material systems (the original focus of percolation theory) and pattern and process relationships within landscapes. The effect of a critical threshold may be easier to visualize by imagining the process of habitat loss and fragmentation. If a landscape exists with $p = 1.0$—that is a landscape entirely composed of a single land-cover type, say forest—then a gradual reduction in p on a random map is equivalent to poking holes in the forest. As the value of p slowly declines (i.e., the forested lands are randomly converted to other land-cover types) from 1.0 to 0.90, isolated gaps in the continuous forested landscape occur with little effect on the overall landscape pattern. As random clearing continues (i.e., values of p further decline from 0.9 to 0.6), forest gaps become more frequent and larger, the amount of edge increases, but never-the-less a single large forest cluster still dominates the landscape. It is still possible for organisms restricted to forests to move across the landscape—that is, the single large cluster still percolates. However, the single large cluster becomes more and more dendritic as the critical threshold is approached. It is now possible to find numerous sites that would disconnect the percolating cluster if they were converted from forest. The sudden disconnectance of the forest habitat resulting from the disturbance of a single site is most likely to occur when $p = p_c$.

The numerical value of a critical threshold depends on the neighborhood rule used to identify clusters (Plotnick and Gardner 1993). When an "eight-neighbor" rule is used to identify clusters, the value of p_c drops to 0.40725 (Table 3.1). Because diagonal neighbors are now also counted as cluster members, potential neighbors are further away from each other. With the inclusion of more distant neighbors within the cluster, large dendritic structures form and "percolate" across the grid at lower values of p. The ecological justification for the analysis of landscape pattern with different neighborhood rules should be process dependent. For instance, if the spread of a disturbance is slow and via immediate contact (e.g., some fungal diseases), then the nearest-neighbor rule might be applied and a critical threshold of the spread of the fungus would occur at $p = 0.59275$. However, short distance dispersal of large seeds might cover a neighborhood of considerable area, resulting in a revised definition of connectance among neighboring sites. It may also be necessary to change the neighborhood rule if the resolution of the map were to change. For instance, a four-neighbor rule applied to maps with 90-m grid cells might be

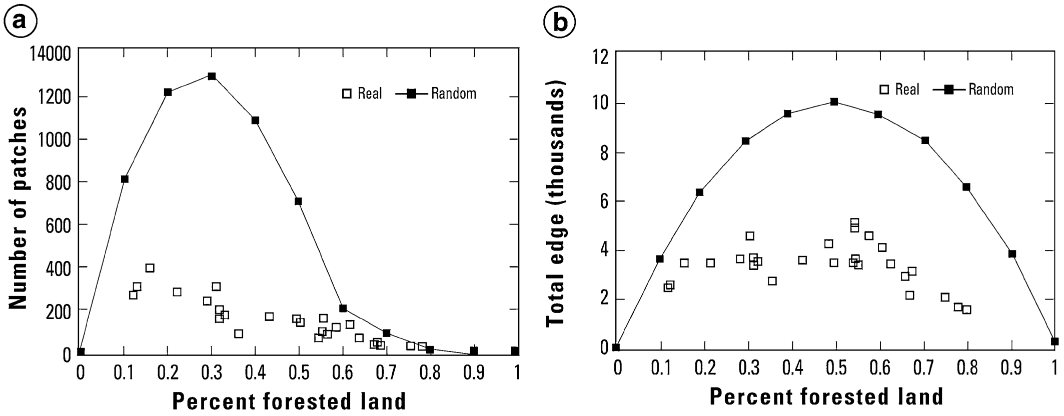


FIGURE 3.8.

Comparison of (**a**) the number of clusters and (**b**) total number of edges for random and actual landscapes.

ADAPTED FROM GARDNER ET AL. (1992B).

changed to a 21-neighbor rule if map resolution were increased to 30 m (other alternatives exist and may be explored in the lab exercises associated with this chapter). The value of the critical threshold has also been shown to vary with map geometry (Table 3.1) primarily because different map geometries have different number of neighbors (e.g., a triangular grid has three neighbors associated with each site while a honeycomb grid would have eight neighbors). Even though the value of the threshold may change, the general response of the system is similar no matter what rule is applied.

One of the initial misunderstandings in the use of random maps as NLMs was the idea that NLMs were intended to represent actual landscape patterns. That was never the case! *NLMs do not represent actual landscapes, but provide the standard against which actual landscapes may be compared.* The NLMs control for the amount of a land-cover type, allowing consequences of particular spatial patterns to be evaluated against the random pattern given comparable habitat abundance. The level and kinds of deviation in spatial pattern compared to random expectations may also help elucidate factors that generate patterns. Thus, it is valid to compare NLMs with actual landscapes—that is, compare patterns generated at random with patterns structured by landscape processes. For example, aerial photographs for nine counties in Georgia taken at three different times and representing different physiographic regions (Turner and Ruscher 1988) were used to develop 27 landscape maps. The number of clusters and total edge of forested areas were compared to NLMs (Gardner et al. 1992; Fig. 3.8). A number of points illustrated by this comparison have been subsequently confirmed by analysis of data from other areas (Gardner et al. 1993). The key points are:

1. It is trivially true that patterns of random and real landscapes are identical when p is equal to either 0.0 or 1.0. It is important to remember that the nearer the value of p is to these limits the more similar random and real landscapes become.
2. The total number of clusters of actual landscapes and NLMs is greatest when p is within the range of 0.1–0.3. Over the range of $p = 0.1$–0.5 the total number of clusters in actual landscapes is noticeably less than that of NLMs.
3. In actual landscapes and NLMs the total amount of edge is at a maximum near $p = 0.5$, but like the cluster numbers, the amount of edge in actual landscapes is much less than in random ones.
4. The degree of connectivity (as measured by the presence of a single cluster spanning the map) was equivalent to the NLMs in 25 of 27 actual landscapes. The two landscapes which differed from NLMs either percolated at $p = 0.43$ or failed to percolate at $p = 0.68$. The cause of this deviation was due to the interaction of topography (ridge and valleys) and the process of human land-use conversion.

The qualitative trends in pattern in actual landscapes and NLMs are similar although the magnitude (e.g., number of clusters, amount of edge) is less and the variability greater in actual landscapes. These differences are produced by a complex suite of factors that organize patterns on actual landscapes (Chap. 2).

An important and very practical application of NLMs has been their use to test the performance of different landscape metrics (Li et al. 2005; Gardner and Urban 2007; Wang and Malanson 2007) across a range of conditions (i.e., number of habitat types, map sizes, values of p). The evaluation of spatial indices by NLMs before they are applied to actual landscapes, and the systematic comparison among similar landscape indices, provides important information on the reliability of different metrics to identify unique patterns on actual landscapes (Gardner and O'Neill 1990; Gustafson and Parker 1992; Gardner and Urban 2007; Nesslage et al. 2007). We revisit this topic in Chap. 4, but several lessons from these studies are worth highlighting here. The first is that the value of p (i.e., the amount of any land-cover type of interest) affects the value of nearly all landscape metrics. Indeed p often enters directly into the calculation of the metric itself (e.g., diversity, contagion) or indirectly as an indication of the amount of habitat found on the map. As p increases, the number of possible arrangements of land-cover decreases. Obviously, differences in landscape pattern as a result of differences in p are not surprising. But, the key point is that interpreting the patterns or relating them to processes must first account for the value of p! The second caveat is that the critical threshold causes a transition from many small to fewer large clusters on the map. Therefore, large differences in landscape metrics should be expected above and below this critical threshold. It is questionable whether metrics insensitive to this transition will provide useful insight into landscape pattern and process. Finally, it is quite clear that the introduction of new indices without prior testing by a series of neutral models should be regarded as a serious omission.

Correlated Patterns from Fractal Maps

Landscapes composed of multiple habitat or land-cover types may require a more complex neutral model to characterize these patterns. Often the arrangement of multiple land-cover types is directly linked to the topography of the region; wetlands and riparian forests are usually associated with rivers and floodplains and found at lower elevations, whereas drier conditions and habitats occur along ridge tops. Conditions between these extremes are intermediate in elevation and usually intermediate in soil moisture and temperature levels. Because habitat characteristics (land-cover types) vary with these elevational gradients, many landscapes with multiple cover types are characterized by a strong autocorrelation between habitat types. Methods that can generate patterns of continuous change would provide a useful neutral model for landscapes with multiple land-cover types.

One method for representing continuous, autocorrelated variation of patterns is the generation of maps via fractional Brownian motion. A fractal Brownian motion in one dimension is produced by creating a series of steps, X_t, whose distance from the previous step $(X_{t+1} - X_t)$ is randomly determined from a Gaussian distribution. A 3-dimensional map may be produced by allowing steps to occur in both the X and Y directions with the random displacements recorded as elevation (the Z direction). The midpoint displacement method (MPDM) for creating fractal surfaces has been extensively used to model 3-dimensional patterns (Barnsley et al. 1988). The "fractal" of fractional Brownian motion is controlled by two parameters: The variance of displacement of points, σ^2 (usually set to 1.0), and H, which controls the correlation between successive steps (Saupe 1988; Plotnick and Prestegaard 1993). Because the successive displacement of points results in an expected difference between any two points equal to $(E[X_1 - (X_1 - d)] \propto d^{H}$ (Plotnick and Prestegaard 1993), the difference between two points will be proportional to the square of the distance, d, and the correlation, $C(d)$, between the points $[C(d) = 2^{2H-1} - 1]$ (Mandelbrot 1983; Feder 1988). The fractal dimension, D, of maps generated by the MPDM is equal to $D = 3.0 - H$ (Saupe 1988). When $H = 0.5$, successive displacements in the Brownian walk are not correlated; when $H < 0.5$, successive displacements are negatively correlated and maps appear to have a very rough surface; and when $H > 0.5$ steps are positively correlated and the maps have a smooth surface (Fig. 3.9). Habitat maps may be generated from the continuous numbers produced by the MPDM by scaling the real numbers and assigning ordinal values to each grid square proportional to the fraction of the map, p_i, occupied by each habitat type (Gardner 1999, 2011). This process of generating a neutral model with fractal maps is summarized in three steps: (1) generation of a topographic map with roughness controlled by H; (2) slicing the topography into contours with the area of each contour equal to the proportion of the map occupied by that habitat type; and (3) assigning ordinal habitat (land-cover) values to sites within each contour.

The realistic nature of the fractal maps is the direct result of the autocorrelated process of map generation (Fig. 3.9) which results in realistic associations between habitat types (i.e., riparian forests will not be found along ridge tops). Although the patterns are constrained by this autocorrelation resulting in frequency distributions of cluster sizes that differ from those of simple random maps, the map patterns produced by fractal methods are still random. The creation of multiple maps with the same set of parameters (map size, H, number of habitat types and the value of p for each habitat) produces dramatically different patterns. However, successive habitat types will always be associated with each other. The positive autocorrelation of maps with high values of H creates larger average cluster sizes than maps with smaller values of H when $p < p_c$ (Table 3.2). Above the critical threshold average cluster sizes are similar among all map types.

The generation of spatial patterns with fractal maps has had a number of applications. Fractal landscapes have been used to represent the degree of spatial dependence of actual landscapes (Milne 1991a, b; Palmer 1992); the effect of landscape fragmentation on population and community dynamics (With et al. 1997; With 2002; With and King 2004); the invasive spread of exotics (Lavorel and Chesson 1995; With 2002, 2004); and landscape disturbances (McKenzie et al. 2006; Wimberly 2006). In most of these examples the effect of "structure" on habitat arrangement was quantified by comparison of fractal maps with simple (nonstructured) random maps. For instance, the objective of With et al. (1997) was to examine how landscape structure affected the patterns of population dispersion of mobile organisms. Variation in landscape structure was created by generating maps that differed in the number and proportion of habitat types and the methods used to generate the spatial patterns. Simple random maps created pattern without an underlying structure, while fractal maps with different values of H created differently structured maps. The results showed that landscape structure had a large effect on the distribution of simulated patterns of species distributions. Although population size remained fairly constant over all simulations, patterns of distribution shifted owing to the aggregation of individuals within specific habitat types. The control of landscape structure created by the comparison of neutral models allowed the effect of pattern and scale to be evaluated.

Pearson and Gardner (1997) used randomly generated fractal landscapes for an entirely different purpose—to determine the consequences of spatial variation in the patterns of ^{137}Cs contamination in a Tennessee reservoir. The spatial

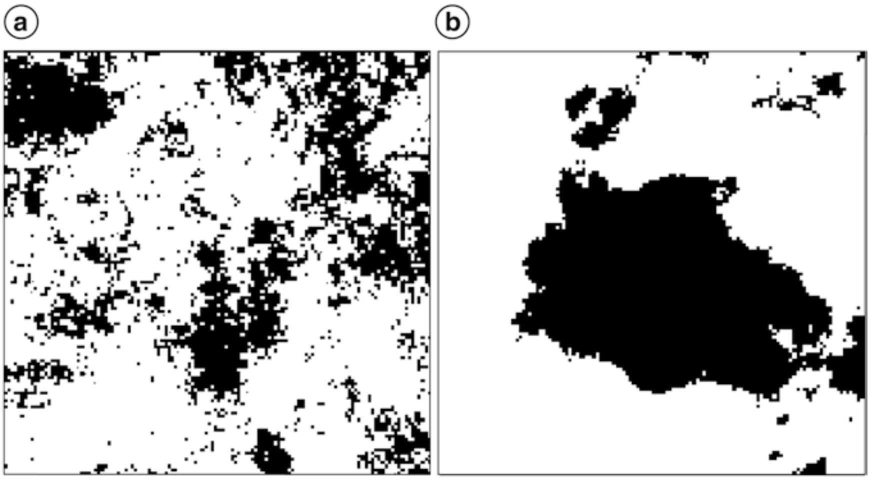


FIGURE 3.9.
Two examples of fractal maps with: (**a**) $H = 0.2$ and (**b**) $H = 0.8$. Each map has 128 rows and columns and the value of p (*green cells*) for each landscape type equals 0.33.

pattern of contamination was important because sites within the reservoir with high contaminant levels ("hot spots") could affect cleanup strategies. It was believed that contaminant hot spots should be spatially correlated, but the degree of correlation was not known. Fractal maps with varying levels of H were produced to assess the effectiveness of various sediment sampling schemes on the detection of these hot spots. The results showed that spatial patterns could be detected accurately in maps with a large degree of spatial autocorrelation using relatively few samples. However, as autocorrelation declined, the number of samples required to achieve the same degree of accuracy increased dramatically. A comparison of fractal maps with ^{137}Cs distributions estimated by a sedimentation model showed that contaminant levels were positively correlated within deposition zones (i.e., areas with similar hydrodynamics), but uncorrelated across different deposition zones.

Other applications of fractal landscapes as neutral models have included the effect of pattern on dispersal (Walters 2007), exploration of edge effects (With 1997; With et al. 1997) and source-sink relationships (Milne 1992; With 1997). Because multiple realizations of these neutral models can be generated, systematic application allows the effect of one component of landscape structure—the autocorrelation among habitat types—to be determined.

INSIGHTS AND APPLICATIONS OF NLMS

The most influential conceptual contribution of NLMs to landscape ecology revolves around the existence of critical thresholds—and the implications of these thresholds for relating landscape pattern to ecological processes (Homan et al. 2004; Groffman et al. 2006b). Although landscapes are not random, there are critical thresholds in connectivity where sudden changes in landscape pattern may occur with small shifts in disturbance regimes or changes in land-use. The factors that organize actual landscapes are not random making the prediction of the exact value of p_c for any given landscape uncertain (see Discussion Question 6.3). Never-the-less, critical thresholds for real landscapes do exist! Thus, above p_c we can expect landscape pattern to be dominated by a single very large cluster, while landscapes with values of p below p_c will be characterized by numerous, smaller, fragmented patches. Shifts in pattern that result from small changes in land-use may cross this threshold and have important implications for metapopulation dynamics and conservation of species diversity (Dale and Zbigniewicz 1995; Pearson et al. 1996; Gardner and Engelhardt 2008; also see Chap. 8). Metapopulation dynamics are possible in landscapes below p_c, while a single, large population dominates can occur in landscapes where the amount of habitat is above p_c. Conservation efforts should be cognizant of the implications of critical thresholds and connectivity in actual landscapes. Because small changes in available habitat near the critical thresholds result in disproportionately large changes in the degree of landscape fragmentation, efforts to preserve continuous tracts of habitat are highly vulnerable to disturbance effects when the amount of habitat is near the critical threshold.

A second key insight from NLMs is that the amount of habitat on a landscape (so the value of p) will strongly influence the values of a wide array of landscape metrics (see Chap. 5). Stated simply, habitat amount constrains habitat pattern, or composition affects configuration. Other related lessons learned from NLMs include:

- *Map dimensions*: Map boundaries affect pattern by the truncation of map patches. The truncation effect becomes more serious as map dimensions decline and p increases. Patterns for maps that are smaller than 100 rows and columns may be seriously impacted by these truncation effects.
- *Patch Structure*: Simple random maps have the greatest number of patches, with the number of patches determined by p. When patterns with contagion are generated (i.e., positive or negative associations between sites on the map), then the number of patches decreases. For instance, curdled maps generally have fewer patches than random maps because the hierarchical structure of map generation affects the contagion between map sites.

- *Thresholds of Connectivity*: Simple random maps are likely to have a single cluster which spans the map (percolates) when $p \sim 0.6$. Random maps with very high or very low contagion will percolate at $p > 0.6$. Random maps with moderate levels of contagion will percolate at $p < 0.6$. When a landscape is above the threshold of connectivity, patches tend to be large and contiguous and there is less difference among patterns. When a landscape is below the threshold of connectivity, patches tend to be small and fragmented and there may be greater differences between different maps. For instance, curdled maps can percolate when the overall value of $p \sim 0.6$, but each level must also percolate. On all maps (random or real), the probability of percolation is directly related to the size of the largest patch.
- *Connectivity and Scales*: Connectivity of sites across a map is defined by the relationships between map pattern and the process of interest, which "connects" adjacent sites. Therefore, connectivity is directly related to habitat abundance (p), the spatial arrangement of suitable habitat, and the resource utilization "rule" of the process being considered. On random maps, thresholds in connectivity occur near 0.6, 0.35, and 0.25 for successively larger neighborhoods of 4, 8, and 12 neighbors, respectively. Connectivity may be expected to vary most at intermediate levels of habitat abundance (e.g., 0.3–0.6).

Practical applications of NLMs often involve their coupling with dynamic ecological models that seek insight into the relationships between pattern and process within heterogeneous landscapes. The NLMs provide replicated manifestations of patterns from which measures of central tendency and variance can be obtained. The ability to generate replicate maps creates a control over the variation in spatial heterogeneity that simply is not possible with traditional sampling. The application of NLMs to landscape issues seems limited only by imagination, and is certainly an economical precursor to more expensive empirical studies. However, the use of NLMs for landscape studies also generated misunderstandings, and several caveats for the use of neutral models (with and King 1997; Gardner and Urban 2007) are important:

- Agreement of a NLM with a set of observations is not proof that the NLM is true (Caswell 1976). Agreement may suggest hypotheses that can be experimentally tested to establish their validity.
- The lack of agreement between an NLM and a set of observations does not prove that the excluded processes are responsible for the observed pattern (Caswell 1976).
- NLMs are theoretical constructs that may not be directly applicable to actual landscapes. For instance, it would be a misuse of NLMs to design a conserva-

tion reserve with the proportion of habitat equal to 0.59275. “On the other hand, approaching the design of the reserve with an appreciation of the importance of connectivity … would be an appropriate application (With and King 1997).”

- It is a misunderstanding of the role of NLMs to reject them as “artificial” and hence misleading simply because they fail to be good predictors of a particular ecological process (see Schumaker 1996; Gardner and Urban 2007). No single NLM will be appropriate for all situations. Rather the NLM should be designed to provide the appropriate null hypotheses against which actual patterns may be tested.

SUMMARY

A model is an abstraction or representation of a system or process. There are many different kinds of models, and mathematical models are commonly used in ecology. In landscape ecology, model development is an important tool that complements empirical techniques. Models permit the landscape ecologist to explore a broader range of conditions than can usually be set forth experimentally. Landscape models help to formalize our understanding and develop theory about how spatial patterns and processes interact, producing general insights into landscape dynamics.

Models are characterized in various ways: for example, models may be deterministic or stochastic; analytical or simulation; dynamics or static; and represent time as continuous or discrete. A model is spatial when the variables, inputs, or processes have explicit spatial locations represented in the model. A spatial model is only needed when explicit space—what is present and how it is arranged—is an important determinant of the process being studied.

The process of building a model is multifaceted and includes the following steps illustrated in Fig. 3.2: (1) Define the problem. (2) Develop the conceptual model. (3) Select the model type. (4) Develop the model by writing out the mathematical equations and relationships. (5) Computer implementation, including verification and documentation of the code. (6) Estimate the parameters, and calibrate if necessary. (7) Evaluate the model by comparison with empirical observation and perform a sensitivity or uncertainty analysis. (8) Use the model for experiments and prediction.

Models are and will remain extremely important tools in landscape ecology. Wise application of these models requires care, however, particularly to the following points: (1) Performance of any model results from the hypotheses and assumptions on which it is built. Comparing alternative model formulations is extremely valuable. (2) Understanding the sensitivity of models to error in estimating parameters is critical; however, assessing error propagation in spatial models remains challenging. (3) All models are simplifications of reality, and the domain of applicability for each model must be defined. (4) Gaps in empirical data for estimating key parameters are often a great source of uncertainty in model predictions. The empirical database that contributes to a model must be understood. (5) Technologically advanced methodologies do not assure the accuracy or reliability of model results!

A NLM is any model used to generate pattern in the absence of specific processes being studied. Predictions from NLMs are not intended to represent actual landscape patterns, but rather define the expected pattern in the absence of a specific process. Comparison of the results of NLMs against actual landscapes provides a standard against which measured departures may be compared. If real landscapes do not depart from a NLM then there may be no need for a more complex model. The types of NLMs that may be generated are diverse (see Keitt (2000) for a unified approach to the generation of NLMs). Random maps provide the simplest NLM, but more complex neutral methods including hierarchical random maps and fractal maps have been used to provide insight into the effect of structured patterns of land-cover on ecological dynamics.

Studies utilizing NLMs have been important in the development of theory and the testing of methods for the analysis of landscape patterns. Results of these studies have been helpful for exploring the implications of landscape patterns for ecosystem processes, population dynamics, disturbances, management decisions, and conservation design. Neutral models are particularly useful for testing differences between landscapes when experimental manipulation and/or replication is not feasible and also serve as an economical means for designing expensive empirical studies. NLMs also played an important role in the development of theoretical landscape ecology by identifying critical thresholds in landscape connectivity, and they have been crucial for understanding the behavior of metrics of landscape pattern NLMs will continue to have a role in landscape studies because of the challenges associated with manipulating spatial patterns in broad-scale empirical studies.

DISCUSSION QUESTIONS

1. What are the distinguishing characteristics of landscape models? What is the difference between a spatially explicit and spatially implicit landscape model? Must all landscape models be spatially explicit?
2. What are the trade-offs (advantages and disadvantages) to using simple vs. complex models?

3. The survey of recent models presented in this chapter provides an overview of current modeling activities. Are models being applied in a balanced manner to the broad spectrum of landscape issues? What areas of landscape ecology are missing from the list of topics reviewed? Why?
4. Technological advances now allow complex spatial simulations to be easily performed and often linked with GIS software to produce mapped output. What should be the key concerns of landscape ecologists for the development, analysis, and application of these methods?
5. The statement was made in the text that "…it is not surprising that a (simple random) map one-half the size of another will have an average cluster size that is only one-quarter as large." Provide an algebraic proof that this will always be the case for simple random maps when $p > p_c$. Is this a scaling rule? Explain why this is not the case for simple random maps when $p < p_c$ (see Table 3.2).
6. Can theoretical or empirical rules relating pattern to map size be defined for fractal maps? If not, how would you go about establishing an empirical scaling rule for fractal maps?
7. Percolation theory predicts a critical threshold when $p \geq 0.59275$. What are the assumptions behind the use and application of this value? Do these assumptions apply to actual landscapes?
8. Table 3.2 shows that average cluster sizes of random and fractal maps are nearly the same when $p = 0.7$ or 0.9. Why is this true? Will other measures of landscape pattern also be similar for these values of p? Will the effects of landscape change be undetectable unless p falls below the critical threshold?

APPENDIX: CLASSIFICATION OF MODELS

Models may be described or classified in various ways, and it is helpful to understand some commonly used terms. We review the terms often used to describe ecological models; similar distinctions are also presented by Grant et al. (1997).

Deterministic vs. *stochastic*. A model is deterministic if the outcome is always the same once inputs, parameters, and variables have been specified. In other words, deterministic models have no uncertainty or variability, producing identical results for repeated simulations of a particular set of conditions. However, if the model contains an element of uncertainty (chance), such that repeated simulations produce somewhat different results, then the model is regarded as stochastic. In practice, the heart of a stochastic simulation is the selection of random numbers from a suitable generator. For example, suppose that periodic movements of an organism are being simulated within a specified time interval. It may be likely that the organ-

TABLE 3.3.
TERMINOLOGY FOR MODEL COMPONENTS AND COMMON PROCEDURES.

Term	Definition
Parameter	A constant or coefficient that does not change in the model
Variable	A quantity that assumes different values in the model
State variable	Major elements of the model whose rates of change are given by differential equations
Initial conditions	The values of the state variables at the beginning of a simulation
Forcing function, external variable, or driving variable	Function or variable of an external nature that influences the state of the system but is not influenced by the system
Output variables	Variables that are computed within the model and produced as results
Sink	A compartment in the model into which material or flow goes, but from which it does not return
Source	A compartment from which the material flowing in the model flows, but to which it does not return
Dimensional analysis	The process in which the units in a model are checked for consistency
Calibration	The process of changing model parameters to obtain an improved fit of the model output to empirical data
Corroboration	The process of determining whether a model agrees with the available data about the system being studied
Sensitivity analysis	Methods for examining the sensitivity of model behavior to variation in parameters
Validation	Term commonly used for the process of evaluating model behavior by comparing it with empirical data; we prefer corroboration because it does not imply "truth"
Verification	The process of checking the model code for consistency and accuracy in its representation of model equations or relationships

ism will move, but it is not certain when this event will occur. One solution is to represent the movement event as a probability, say 0.75, and the probability of not moving as (1.0–0.75) = 0.25. Selection of a random number between 0.0 and 1.0 is done to "decide" randomly if movement occurs during a specific time interval. If the simulation is repeated, the time-dependent pattern of movement will be different, although the statistics of many movement events will be quite similar. Inclusion of stochastic events within a model produces variable responses across repeated simulations – a result that is quite similar to our experience of repeated experiments.

Analytical vs. *simulation*. These terms refer to two broad categories of models that either have a closed form mathematical solution (an analytical model) or lack a closed form solution and therefore must rely on computer methods (a simulation model) to obtain model solutions. For analytical models, mathematical analysis reveals general solutions that apply to a broad class of model behaviors. For instance, the equation that describes exponential growth in a population is an example of an analytical model (Table 1), as are many of the model formulations used in population ecology (May 1973; Hastings 1996).

In contrast, the complexity of most simulation models means that these general solutions may be difficult or impossible to obtain. In these cases, model developers rely on computer methods for system solution. Simulation is the use of a model to mimic, step by step, the behavior of the system we are studying (Grant et al. 1997). Thus, simulation models are often composed of a series of complex mathematical and logical operations that represent the structure (state) and behavior (change of state) of the system of interest. Many ecological models, especially those used in ecosystem and landscape ecology, are simulation models.

Dynamic vs. *static*. Dynamic models represent systems or phenomena that change through time, whereas static models describe relationships that are constant (or at equilibrium) and often lack a temporal dimension. For example, a model that uses soil characteristics to predict vegetation type depicts a relationship that remains the same through time. A model that predicts vegetation changes through time as a function of disturbance and succession would be a dynamic model. Simulation models are dynamic.

Continuous vs. *discrete time*. If the model is dynamic, then change with time may be represented in many different ways. If differential equations are used (and numerical methods available for the solution) then change with time can be estimated at arbitrarily small time steps. Often models are written with discrete time steps or intervals. For instance, models of insects may follow transitions between life stages; vegetation succession may look at annual changes, etc. Models with discrete time steps evaluate current conditions and then "jump" forward to the next time while assuming that condition remains static between time steps. Time steps may be constant (i.e., a solution every week, month, or year) or event-driven, resulting in irregular intervals between events. For example, disturbance models (e.g., hurricane or fire effects on vegetation) may be represented as a discrete time-step, event-driven model.

Mechanistic, process-based, empirical models. These three terms are frequently confusing. A "mechanism" is "...the arrangement of parts in an instrument." When used as an adjective to describe models (i.e., a *mechanistic* model) the term implies a model with "parts" arranged to explain the "whole." In the best sense of the term, a "mechanistic" model attempts to represent dynamics in a manner consistent with real-world phenomena (e.g., mass and energy conservation laws, the laws of chemistry, etc.). Although there has been waning support for mechanistic approaches to ecological modeling (Breckling and Muller 1994), the use of "mechanistic" in the strictest sense distinguishes these models from "black box" models which grasp at any formulation which might satisfactorily represent system dynamics. Confusion arises when the term "mechanistic" is loosely applied to distinguish less detailed models from more detailed ones. Often the implication is that mechanistic models are more desirable than less mechanistic(less detailed) models. Unfortunately, the assertion that additional detail produces a more reliable model must be demonstrated on a case-by-case basis (Gardner et al. 1982).

A "process-based" model implies that model components were specifically developed to represent specific ecological processes—e.g., equations for birth, death, growth, photosynthesis, and respiration are used to estimate biomass yields rather than simpler, more direct estimates of yields from the driving variables of temperature, precipitation, and sunlight. Although this concept seems clear, there is no a priori criterion defining formulations which qualify (or conversely do not qualify) as process models. Thus, depending on the level of detail, it is possible to have a "mechanistic process-based" model or an "empirical process-based" model.

An "empirical" model usually refers to a model with formulations based on simple, or correlative, relationships. This term also implies that model parameters may have been derived from data (the usual case for most ecological models). Regression models (as well as a variety of other statistical models) are typically empirical because the equation was fitted to the data.

The problem of distinguishing between types of model is illustrated by the simulation of diffusive processes based on well-defined theoretical constructs (Okubo 1980). These formulations of diffusion allow simple empirical measurements to define the coefficients estimating diffusive spread. Thus, there is a strong theoretical base along with empirically based parameters. Is such a model considered empirical or theoretical? Should complex formulations always be considered more theoretical or simply harder to parameterize?

The essential quarrel with each of these three terms is that most ecological models are a continuum of parts, processes, and empirical estimations. Separating models into these arbitrary and ill-defined classifications lacks rigor and repeatability. One person's mechanistic model is the next person's process-based model, etc. There does not appear to be a compelling reason to use these vague and often confusing terms to distinguish between alternative model formulations.

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CHAPTER

4

LANDSCAPE METRICS

Studies in landscape ecology are concerned with determining the causes, consequences, and functional importance of spatial heterogeneity. Success in accomplishing these ambitious goals requires meaningful, robust methods for quantifying spatial pattern. Landscape ecologists use numerous metrics, and readily available spatial data combined with user-friendly software have made such analyses routine. However, the goal of landscape ecology is not simply to measure landscape pattern, and spatial pattern analysis is but one tool used to unravel the complex phenomena and relationships forming landscapes. Nevertheless, quantifying spatial heterogeneity is a key tool of the trade, and this chapter explains how to select, compute, and interpret landscape metrics. The development of new metrics has slowed (thankfully!), but useful new approaches that have emerged in the past decade are included here. While the nuts-and-bolts of individual metrics and software programs will continue to evolve over time, there are general caveats that apply to any analysis of landscape pattern. We begin this chapter by discussing why pattern is quantified and where landscape data come from, then highlight key caveats and cautions that must be considered *before* landscape pattern is analyzed. We next present commonly used landscape metrics of composition and configuration, introduce surface metrics briefly, and discuss connectivity measures derived from graph theory. Finally, we address the challenges associated with detecting significant differences in metrics and interpreting multiple pattern metrics, then proffer some added practical advice. This chapter largely focuses on pattern analysis based on categorical data, and we cover spatial statistics in the next chapter.

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WHY QUANTIFY PATTERN?

Because landscape ecology emphasizes the interaction between spatial pattern and ecological process, methods by which spatial patterning can be described and quantified are necessary. There are numerous practical examples of where quantitative understanding of the pattern is important. First, landscapes change through time, and we may be interested in knowing whether the pattern is different at time $t+1$ than it was at time t. Furthermore, we may want to know specifically *how* landscape pattern has changed. Landscapes have undergone substantial change during the past two centuries, as illustrated by the changes in John Curtis' classic study of forest cover in Cadiz Township, Wisconsin (Fig. 4.1). Here, we observe

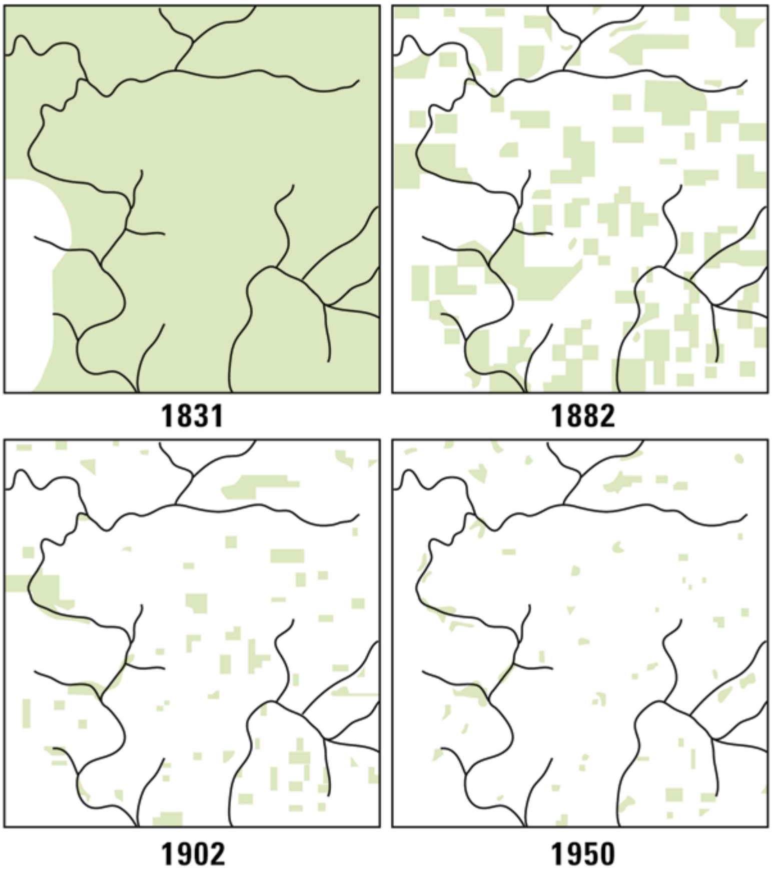


FIGURE 4.1.

Changes in forest cover (*shaded green*) since the time of European settlement for Cadiz Township in southeastern Wisconsin. This pattern can be observed in many areas and illustrates both the changes in the abundance and spatial arrangement of forest in the landscape.

ADAPTED FROM CURTIS (1956).

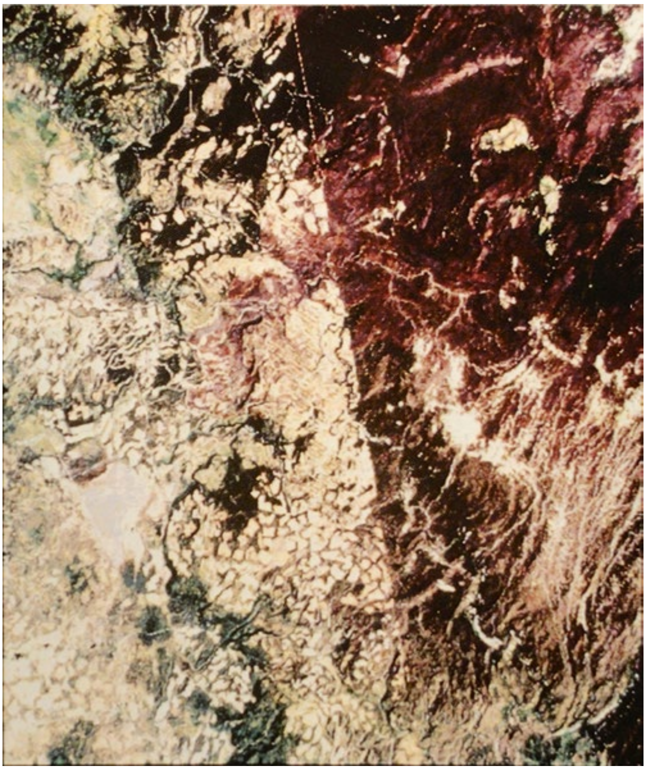


FIGURE 4.2. Differences in landscape pattern are apparent along the western boundary of Yellowstone National Park in this false-color aerial photo. The national park lands with relatively continuous forest cover (in *red*) can be seen to the right. To the left, areas with dispersed patches of clearcuts (*white*) on National Forest and private lands are evident.

that the area of forest has declined through time, and forest patches have become smaller and more isolated. Second, we may wish to compare two or more different landscapes or areas within a given landscape and determine how different or similar they are. In some cases, a political boundary may result in dramatically different landscape configurations within close proximity, as seen along the western boundary of Yellowstone National Park, Wyoming (Fig. 4.2). Numerous small, dispersed clearcuts are evident to the west, where timber was harvested on the national forest, whereas forest is more continuous to the east, within the park. Landscape metrics allow us to determine whether spatial patterns have changed over time, or whether landscapes are different or similar in pattern. Third, when considering the effects of different drivers on landscape pattern or future scenarios, we may need to evaluate quantitatively the different landscape patterns that result. Spatial analyses have been especially informative for detecting differences in landscape pattern associated with different categories of landowner (Fig. 4.3). Finally, different aspects of spatial pattern in the landscape may be important for processes such as the movement patterns of organisms, the redistribution of nutrients, or the spread of a natural disturbance. That is, relating spatial patterns to ecological processes first requires the means to describe these patterns. Consequently, spatial pattern metrics play a key role in many landscape studies.

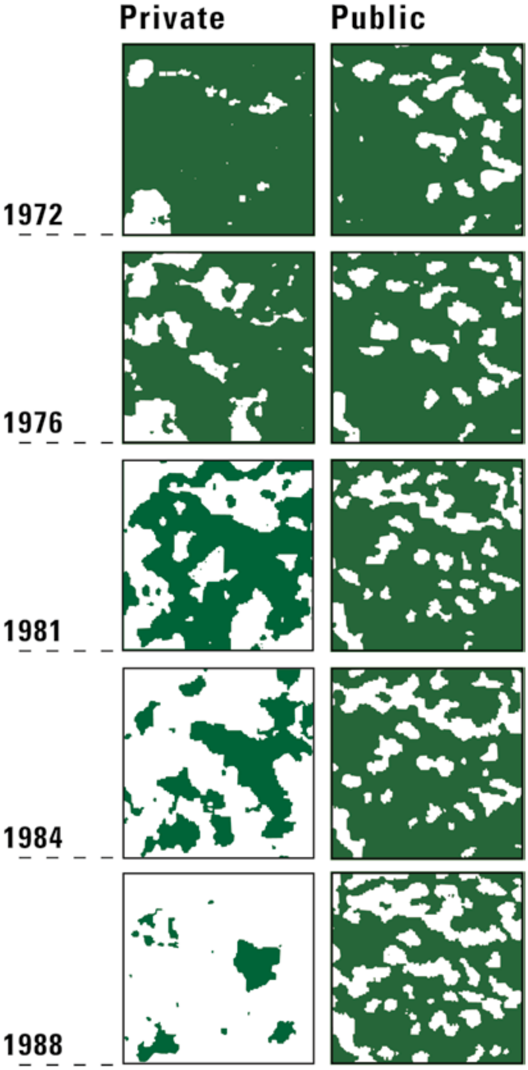


FIGURE 4.3.
Changes in conifer (*green*) and other forest types for a private and public landscape (2500 ha) with similar initial conditions and rates of change that are relatively high for the ownership types. Landscape metrics were used to quantify the differences in landscape pattern between ownerships. Redrawn from Spies et al. (1994).

Spatial analysis received a lot of attention as the concepts and methods of landscape ecology were first emerging in the 1980s (e.g., Romme 1982; O'Neill et al. 1988a). It is notable that even simple patterns can be difficult to describe quantitatively. Methods that are standard today were only being developed "back in the day" when researchers wrote their own computer code to compute and evaluate landscape pattern indices (e.g., Gardner et al. 1987; Baker and Cai 1992; Turner 1990). The development of metrics used with categorical data has largely stabilized, and the analyses are now easy to perform. Practitioners are now expected to understand the methods, use them appropriately, and draw proper inference from the results. It is important to be facile with the quantitative analysis of landscape pattern and to understand the factors that influence the interpretation of landscape metrics.

DATA USED IN LANDSCAPE ANALYSES

Many analyses of landscape pattern are conducted on land-use/land-cover data that have been digitized and stored within a geographic information system (GIS). Four general classes of data are most common.

1. *Aerial photography* remains an important data source for landscape studies, particularly for detecting changes in a landscape during the twentieth century (before satellite data became available) or for examining patterns at fine scales. Black-and-white aerial photos are generally available back through the 1930s, although the quality and spatial coverage may be uneven. More recent aerial photos may be in true color or infrared, and depending on the source, the resolution may be very high. Once any geographic errors in the data are rectified, an analyst usually demarcates the features of interest manually (e.g., Fig. 4.4), which is a very time-intensive process.
2. *Digital remote sensing* data are now widely used and accessible to many researchers. The US Landsat and French Spot satellites have provided frequent and spatially extensive coverage worldwide and are a very useful source of digital data. These data were relatively expensive for many years, but the recent open access (for free) to the archive of Landsat imagery has facilitated numerous studies. For questions that are at regional-to-global scales, MODIS data are also widely used. Airborne imaging scanners (e.g., Lidar or hyperspectral imagery) may be used to provide fine resolution data for a particular locale. Readers should consult a remote sensing text (e.g., Richards and Jia 2006; Mather and Koch 2011) for more detail on these data sources.
3. *Published data and censuses* provide another valuable source of landscape data, particularly for temporal comparisons that extend back beyond the record of aerial photography. For example, the U.S. General Land Office Survey data have been used extensively to describe vegetation prior to European settlement (e.g., White and Mladenoff 1994; Delcourt and Delcourt 1996; Friedman et al. 2001) and methods are available to improve the accuracy of spatially extensive reconstructions (e.g., Williams and Baker 2011). In some areas, other historical mapping efforts also provide data that can be used to infer landscape patterns prior to the advent of aerial photography (e.g., the Bordner Survey in Wisconsin, USA, provided data for the 1930s; e.g., Bürgi and Turner 2002).
4. *Field mapped data* may be used for landscapes of smaller extent in which the investigator might map the spatial patterns of particular vegetation classes or landscape elements of interest in a relatively small area. Field mapping is not generally feasible for studies that cover a large area (e.g., hundreds to thousands of ha). However, it may be the only way to assess patterns in certain habitats, such as coastal benthic communities (e.g., Teixido et al. 2002, 2007).

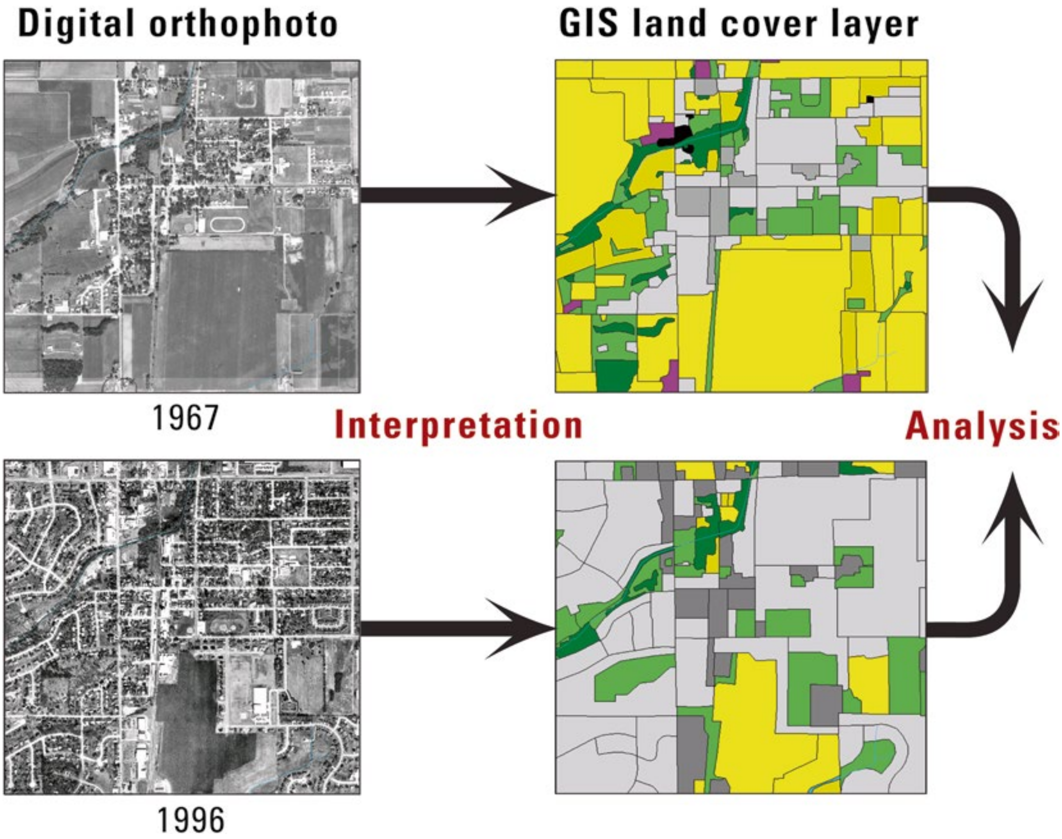


FIGURE 4.4
Example of aerial photography of the same location in the Yahara Watershed, near Madison, Wisconsin, for two different years (1967 and 1996) and the resulting classification of land cover used in an analysis of landscape change over time. Photos on the *left* were orthorectified to correct for geographic distortion and/or misregistration. Images on the *right* show the categorization of these photos into land-cover classes. *Colors*: agriculture = *yellow*; suburban = *gray*; forest = *green*

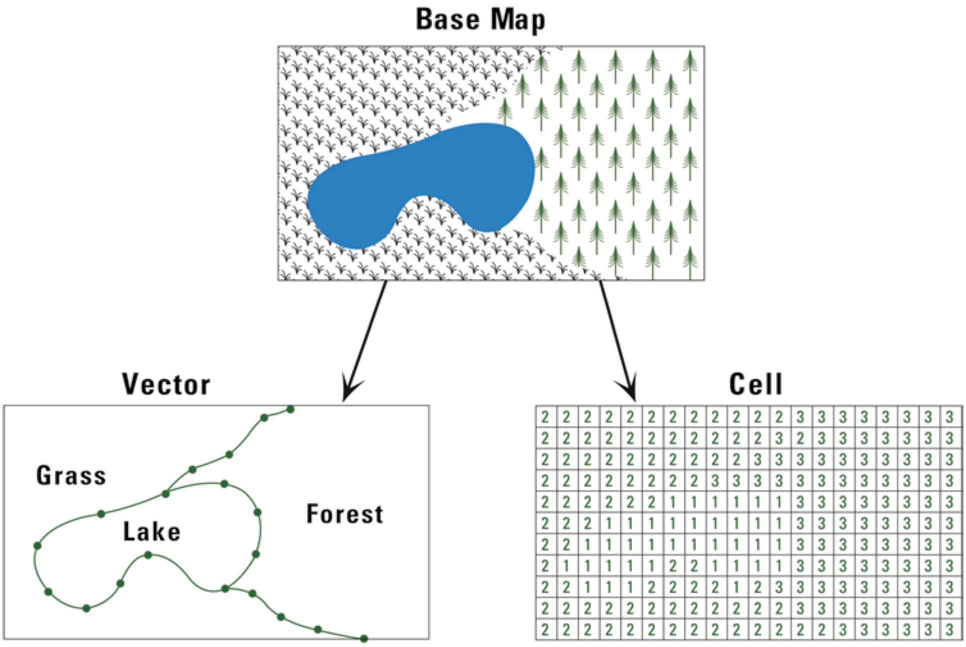
Whatever the selected data source, landscape metrics are generally computed on a spatial dataset in which the images or spectral data have been classified into some meaningful number of categories. In other words, a digital categorical map provides the baseline for the analysis. The land-use and land-cover scheme developed by the US Geological Survey (Anderson et al. 1976) and used for products such as the 1992 and 2001 US National Land Cover Dataset (NLCD, see http://www.mrlc.gov/; Vogelmann et al. 2001; Fry et al. 2009) is a widely used protocol and serves as an example. This scheme is a hierarchical arrangement of categories from general to specific (Table 4.1). For example, forest (a Level I of the Anderson classification system) may be subdivided into deciduous, evergreen, or mixed forestland (Level II). Further divisions (Level III) would distinguish dominant species groups;

TABLE 4.1.
THE USGS LAND-USE/LAND-COVER CLASSIFICATION SYSTEM (ANDERSON ET AL. 1976).

Level I	Level II
1. Urban or built-up land	11. Residential
	12. Commercial or services
	13. Industrial
	14. Transportation, communication, or utilities
	15. Industrial and commercial
	16. Mixed urban or built-up
2. Agricultural land	21. Cropland and pasture
	22. Orchards, groves, vineyards, horticulture
	23. Confined feeding operations
	24. Other agricultural land
3. Rangelands	31. Herbaceous rangelands
	32. Shrub and brush rangelands
	33. Mixed rangelands
4. Forest land	41. Deciduous forest land
	42. Evergreen forest land
	43. Mixed forest land
5. Water	51. Streams and canals
	52. Lakes
	53. Reservoirs
	54. Bays and estuaries
6. Wetland	61. Forested wetlands
	62. Nonforested wetlands
7. Barren land	71. Dry salt flats
	72. Beaches
	73. Sandy areas except beaches
	74. Bare exposed rock
	75. Strip mines, quarries, gravel pits
	76. Transitional areas
	77. Mixed barren land
8. Tundra	
9. Perennial snow or ice	

THIS IS AN EXAMPLE OF A HIERARCHICAL CLASSIFICATION SYSTEM THAT CAN BE USED IN LANDSCAPE ANALYSES.

it is largely the second and third levels that are used in analyses of the NLCD. Landscape data classified into categories are presumed to be homogeneous within a given category—an important assumption that must be recalled when viewing and interpreting these data. There are methods in remote sensing image



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2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3

FIGURE 4.5.

Illustration of the two principal methods for representing spatial data in a GIS: vector-based representation and raster, or cell-based, representation.

ADAPTED FROM COULSON ET AL. (1991).

analysis that do not require the user to determine landscape categories but rather describe the "texture" or "surface" of each image. Most of this chapter will focus on categorical data, but we briefly introduce texture measures.

Most researchers store their landscape data in a GIS for ease of manipulation and display (Fig. 4.5). Many computer programs for landscape analyses were developed for use with raster, or grid cell, data, although vector-based versions are sometimes available. In raster format, a landscape is divided into a grid of square cells of equal size (Fig. 4.5). Other cell shapes (e.g., hexagons) may be used, but square cells are most common because they match many remote-sensed data sources. The size of the grid cell determines the **grain** (resolution) of the mapped data. Irregularly shaped landscapes can be represented within a rectangular perimeter larger than the landscape itself by setting the "background" cells to a value that indicates "no data." In vector format, lines are defined by ordered sets of coordinate pairs defining the boundaries of polygons (Fig. 4.5). The polygons may be of variable size and shape, but the **minimum mapping unit** (i.e., grain size) corresponds to the minimum patch size that was mapped. Raster data are more commonly used in landscape analyses largely because the computer programming of the analyses is easier, and most satellite imagery is in raster format.

A Comment on Spatial Data Accuracy

It is very important to consider the accuracy of the spatial data or map upon which the analysis of landscape pattern is to be performed. Values returned for many landscape metrics will vary with the technique used to process the imagery, and care must be used when comparing results from images with even slight differences in processing methods (Mas et al. 2010). Often, an analyst may be using data classified by other individuals (or institutions), making the accuracy of the original data and subsequent data difficult to establish. Within GIS/remote sensing data, there are a number of recognized potential sources of error (Table 4.2) and every effort should be made to insure that each dataset has minimal error.

Understanding the sensitivity of landscape metrics to error in the input data has received some research attention (e.g., Cardille et al. 1996; Wickham et al. 1997; Langford et al. 2006; Mas et al. 2010), but more is warranted. Using simulated data to propagate error through a landscape change analysis, Burnicki (2012) found that metrics associated with fragmentation were consistently over-estimated and indicated smaller and more variable patches of land-cover change compared to the error-free data. Smoothing algorithms can improve classification error, but it can also have unexpected effects on the landscape metrics and change the direction of the errors (Langford et al. 2006). The key point is that classification error is under reported but can produce inaccurate descriptions of landscape pattern. The old maxim of computer programming, "Garbage in, garbage out," also holds for landscape pattern analysis; the end product is only as good as the data upon which the analysis is based.

CAVEATS FOR LANDSCAPE PATTERN ANALYSIS, OR "READ THIS FIRST"

The widespread availability of spatial data has created myriad opportunities for landscape patterns to be analyzed for many different purposes. It is easy to look up the calculation or equation for any given metric. However, having the framework for the correct use of metrics is critical. Important issues must be addressed before embarking on the analysis of landscape pattern (see Box 4.1). First and foremost among these is having a well-conceived question/rationale for the analysis. It remains easy to fall into the trap of generating a lot of numbers without a clear purpose for the study and recognition of the limitations of the metrics. Reporting metrics is not meaningful without an a priori statement of the objectives of the analysis and/or hypothesized pattern changes (i.e., disturbances will cause a decline in the diversity of land-cover types). Landscape comparisons can also be plagued

Table 4.2.
Sources of potential error in GIS data, adapted from Burrough (1986).

Source	Explanation
Obvious sources	
Age of data	Some data change more rapidly than others, e.g., geological substrate vs. land use. Old data may have been collected under different standards
Aerial coverage	Coverage may be incomplete over a region of interest
Map scale	Does the map scale match the resolution at which the data were originally collected? Is it appropriate for the question?
Political boundaries	Data characteristics may change across political (e.g., county, state) or administrative (e.g., agency, landowners) boundaries on maps formed as a composite
Natural variation in original measurements	
Positional accuracy	Boundary lines or distinctions may not be precisely located due to field mapping or conversion between data formats (e.g., vector to raster) or spatial resolution
Content accuracy	Are the cell attributes correct? In remote sensing interpretation, there are measurable errors associated with classification of the reflectance values
Variation in data sources	Different interpreters may generate different maps; protocols may not be standardized; errors in data entry; natural variability
Processing errors	
Numerical computation	Decimal precision and rounding errors in complex calculations
Topological analyses	When combining map variables or coverages, use of logical operators multiplies errors in individual layers; conversion between vector and raster also may lead to error
Classification	Errors in deriving the category assignments from aerial photos or satellite imagery; error typically estimated for entire map and for each category on the map

by pseudoreplication (Hurlbert 1984; Hargrove and Pickering 1992), which occurs when comparisons are made among samples that are not truly independent. The dangers of pseudoreplication are relevant to landscape ecology because the unique attributes of each landscape make statistical controls difficult and independent replicate samples nearly impossible.

Box 4.1

PRE-FLIGHT CHECKLIST FOR LANDSCAPE PATTERN ANALYSIS

Before embarking on an analysis of landscape pattern, we suggest answering the following questions to guide the analysis and to avoid known pitfalls.

1. What are the scientific or management questions motivating the study?
2. What qualities of spatial pattern are of most interest, and why (i.e., what is the ecological rationale)? How do you expect these qualities to change over time, differ among study areas, or affect processes of interest?
3. Which metrics are potential indicators of the spatial qualities you wish to quantify? Which metrics should be computed for the landscape as a whole, or by cover type, or for individual patches?
4. What spatial data are needed to answer the questions (and are these data available)? Are categorical or continuous data better suited for answering the questions? For categorical data, what classification scheme is appropriate, given the objectives of the study?
5. For analyses involving more than one study area or time period, are scales and classification schemes consistent across datasets?
6. What is the accuracy of the spatial data? Is error in the input data likely to affect the numerical results of the analysis? Are the source data and classification methods consistent when using results to compare landscapes?
7. How is each metric calculated (i.e., what is the equation)? What is its potential range (i.e., minimum and maximum value)? Is it a normalized, or are the values unconstrained? What are the units?
8. What is the correlation structure among the metrics computed in your analysis? (Provide the descriptive statistics of the distributions of each metric, and always check the correlation structure among metrics in your own study by inspecting scatter plots and calculating correlation coefficients!) What is the most parsimonious set of metrics that answers the questions?
9. What method will be used to determine whether metrics (or comparisons made through time or among landscapes) are significant both statistically and ecologically? How will the values, differences or trends of the metrics be interpreted ecologically?

#1 The Classification Scheme Is Critical

The number and type of categories selected for each dataset have a very strong effect on the numerical results of any pattern analysis. For example, consider the pattern of vegetation mapped from remote imagery for the same section of a landscape but classified in different ways (Fig. 4.6). In one case, the vegetation is mapped by forest type, whereas in the other, the vegetation is mapped by forest age. It is clear that these two landscape representations look *very* different and that the quantitative descriptions of these two datasets would be quite dissimilar. Thus, the choice of what categories to include in a pattern analysis is a critical one! The question being asked must drive this selection; that is, the categories must be appropri-

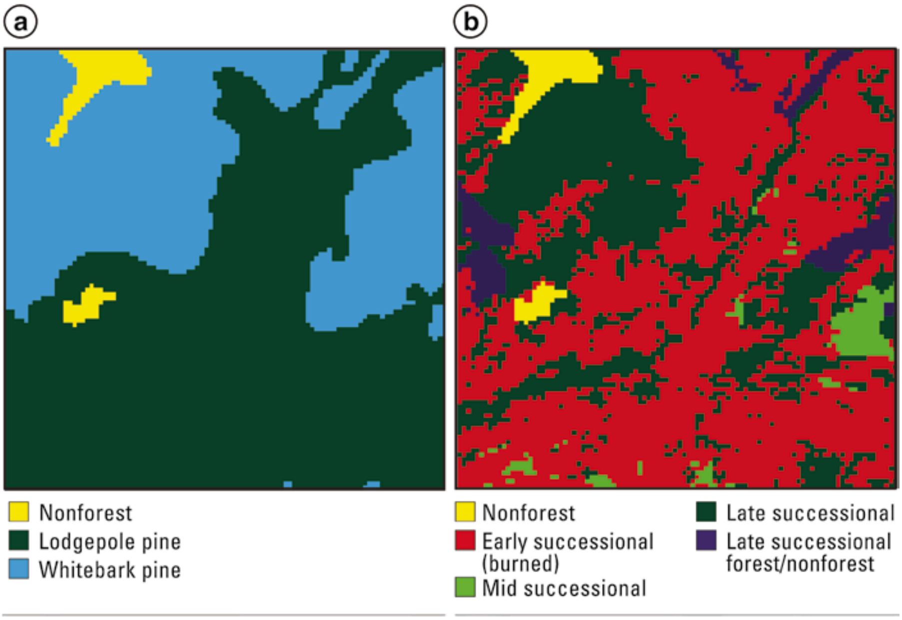

FIGURE 4.6.

Example of how the same landscape looks very different under different classification schemes. Both panels show a 5-km × 5-km section (100 × 100 grid cells) of southwestern Yellowstone National Park. (**a**) The landscape is classified based on the forest community composition. (**b**) The landscape has been classified based on the successional stage of the forest stands.

ate for the objective of the study. For example, general categories (e.g., Level I in Anderson et al. 1976) would be appropriate to study landscape patterns in the eastern USA, but to study vegetation patterns within a forested landscape such as the Great Smoky Mountains National Park, descriptions of a variety of forest community types may be more desirable. Furthermore, the classification scheme must be consistent across all landscapes being compared. For example, to compare changes in landscapes over time (e.g., Fig. 4.4), the categories must be the same, or classes must be aggregated to the level that provides consistency between the datasets. This issue has confounded some analyses of landscape change in the USA using the NLCD data from 1992 and 2001 (Fry et al. 2009).

After the decision is made about what categories to include in a dataset, the interpretation of those categories from a primary data source should be clearly described. For example, the threshold of tree cover used to separate "forest" from "woodland" can vary among classification schemes, as can the density of built structures that distinguish "high-density urban" from "low-density urban" areas. Gustafson (1998) poses the example of studying the distribution of aspen in north woods of Wisconsin

(USA) and needing to specify how much aspen must be present in order to be classified as an aspen stand. The threshold density for classification should be specified, and the use of different density levels among similar maps should be avoided. Each decision in the mapping process will affect the determination and analysis of spatial structure (Gustafson 1998). For others to interpret your findings or compare the results with other studies, the classification scheme must be plain.

#2 Scale Matters and Must Be Defined

The grain and extent of the data used in any analysis of landscape pattern influence the numerical result obtained for a given metric (Turner et al. 1989b; Moody and Woodcock 1995; Wickham and Riitters 1995; Wu 2004; Ostapowicz et al. 2008) and must be defined explicitly. This sensitivity means that comparisons of landscape data represented at different scales may be invalid because results reflect the scale-related errors rather than differences in landscape patterns.

How are landscape metrics affected by scale? As *grain* size increases (i.e., resolution decreases), cover types that are rare on the landscape typically become less well represented or may even disappear (Fig. 4.7). The boundaries between differ-

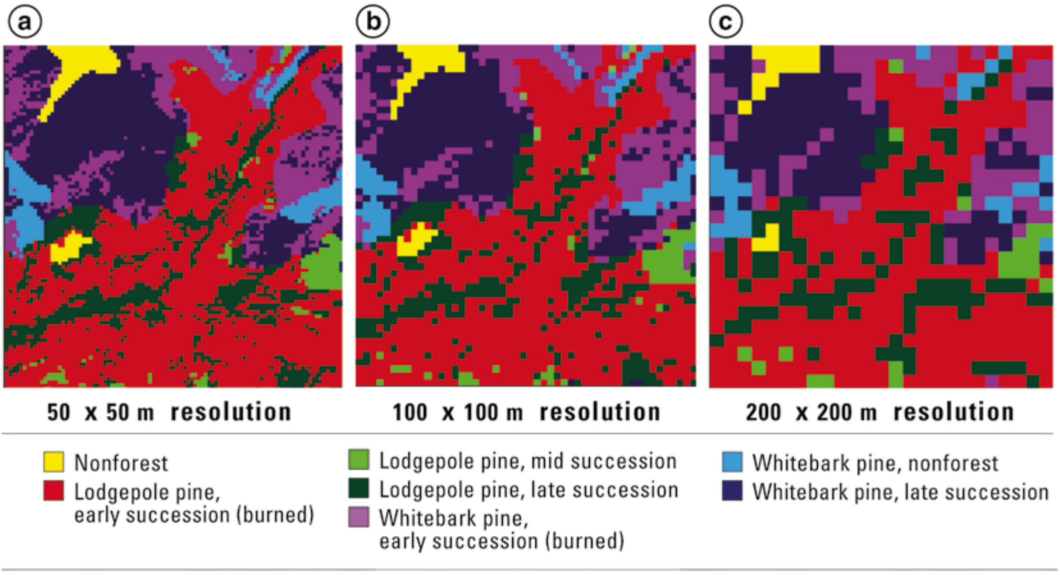

FIGURE 4.7.

Effects of changing grain size on a landscape map. Panels show a 5-km × 5-km section (initially 100 × 100 grid cells) of southwestern Yellowstone National Park aggregated sequentially following a majority assignment rule. (**a**) The original landscape is shown with 50-m × 50-m grid cells. (**b**) Grid cell size is 100 m × 100 m. (**c**) Grid cell size is 200 m × 200 m.

ent cover types also become underestimated with increasing grain size as the shapes depicted become less complex and fine-grained details are lost (Fig. 4.7). By changing grain in a Landsat image from 30 × 30-m to 1 × 1-km, Moody and Woodcock (1995) showed that scale-induced changes in the proportion of the landscape occupied by different cover types influenced landscape metrics including patch size, patch density and landscape diversity. Some metrics are more sensitive to changes in grain size than others. In the Tennessee River and the Chesapeake Bay Watersheds, Cain et al. (1997) found measures of landscape diversity, texture, and fractal dimension were more consistent across analyses in which grain size and the number of cover types varied, whereas measures of average patch shape or compaction were subject to change. Analyses of forest patterns using morphological spatial pattern analysis in Guidos (see Box 4.2) confirmed a strong influence of pixel size on analyses that quantified features related to connectivity (Ostapowicz et al. 2008).

The spatial *extent* of the study area can affect landscape metrics independently of grain size. There are two key effects. First, when landscapes contain multiple cover types, increases in map extent will usually increase the representation of rare cover types, similar to the increases in species with increases in area sampled. The inverse is also true: the number of categories on a map declines with decreasing extent. Second, if patches are large relative to the size of the landscape, patches tend to get cut off by the boundary of the map. The smaller the extent of the map, the more serious this problem of artificial truncation of patches by the map boundary, resulting in biased measurements of patch size, shape, and complexity (Fig. 4.8).

What the minimum map extent should be to prevent serious measurement errors is not always clear. For example, imagine a square landscape of 400 × 400 cells created by the random placement of a single cover type among the grid cells (i.e., a random neutral landscape model; see Chap. 3). Further imagine that the goal of the analysis is to estimate the number of patches in this landscape by sampling with maps of 50 × 50, 100 × 100, or 200 × 200 cells. In the smaller maps, the truncation effect results in consistent overestimation of the total number of habitat patches. However, this bias is small (a maximum of 1.3 % for the 50 × 50 map) for all map sizes when p, the fraction of the map occupied by the single habitat type, is also small. This is because the patches themselves are small and distributed across the landscape. However, when p is greater than 0.6 (i.e., the 400 × 400 map has 60 % of the cells randomly occupied by the single habitat type), sampling bias climbs to 23 %, 9 %, and 3 % for the 50 × 50, 100 × 100, and 200 × 200 maps, respectively. The lessons from this example are: (1) it is difficult to specify *for all* situations what the biases will be for maps of different extent; (2) no single map extent is optimal for all analyses; (3) unless experiments can be performed to evaluate optimal sample sizes, one should sample with maps of the greatest possible extent.

In reporting results from any landscape pattern analysis, the extent and grain size (or minimum mapping unit) of the data must be clearly specified, and compari-

Box 4.2

THE PRACTICAL SIDE: SOFTWARE FOR LANDSCAPE PATTERN ANALYSIS

Getting started in landscape pattern analysis is now relatively easy, given the availability of user-friendly and powerful software programs. We highlight several widely used programs here, all of which are available for free from the developers; new users can also gain hands-on experience with landscape analyses and interpretation by using the second edition of LEARNING LANDSCAPE ECOLOGY (Gergel and Turner 2016).

FRAGSTATS is the most widely used package for landscape pattern analysis (McGarigal and Marks 1995). FRAGSTATS is comprehensive, powerful, easy to use, and the documentation is excellent. FRAGSTATS provides options for calculating metrics over the entire landscape (called "landscape metrics"), by cover type (called "class metrics"), or by individual patches (called "patch metrics"). Version 4 also includes texture measures. Users interested in running landscape analyses might begin with FRAGSTATS <http://www.umass.edu/landeco/research/FRAGSTATS/FRAGSTATS.html>.

Conefor Sensinode is used widely to quantify the importance of individual habitat areas (i.e., patches) and the links among them to assess landscape connectivity (Saura and Torné 2009). Conefor includes an array of connectivity indices and was designed specifically to address landscape conservation questions <http://www.conefor.org/>.

Guidos is a graphical user interface for performing "morphological spatial pattern analysis" of an input image. It focuses especially on structural connectivity and identifying different classes of image components, including core areas, islets, perforations, edges, loops, bridges, and branches. Conefore Sensinode also is included within Guidos. The software can be downloaded from the European Commission Joint Research Centre <http://forest.jrc.ec.europa.eu/download/software/guidos>.

QRULE (Gardner 1999; Gardner and Urban 2007) is a FORTRAN-based program that allows users to generate a variety of different neutral landscape models and analyze the patterns of each landscape, and it can also provide the same analyses for user-input maps. QRULE is the current derivative of the program written by Gardner to generate the first neutral landscape models (Gardner et al. 1987) <http://www.umces.edu/al/program/gardner/Qrule>.

Geospatial Modelling Environment (formerly HawthsTools) are a useful set of tools that allows data structures developed within ArcGIS™ to be analyzed with a wide range of statistical tools available within R <http://www.spatialecology.com/gme/index.htm>.

METALAND is a database of landscape metrics that were already computed in FRAGSTATS for contiguous 6.5 km × 6.5 km landscapes ($n = 193{,}705$) of the 8-million km^2 conterminous USA (Cardille et al. 2005). This searchable database includes land-use/land-cover maps for 1992 and 2001 and allows users to retrieve landscapes that match stated criteria for multiple landscape metrics <http://132.216.21.101/currentprojects/metaland/index.php>.

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sons among landscapes must control for any differences in scale. When grain sizes differ, one approach is to re-sample the fine-scale data to the coarser grain; often, this is done by assigning the category of the majority of the smaller cells to the single larger cell. When landscapes differ in extent and/or shape, normalizing metrics by area often allows comparison of many common metrics. This often entails

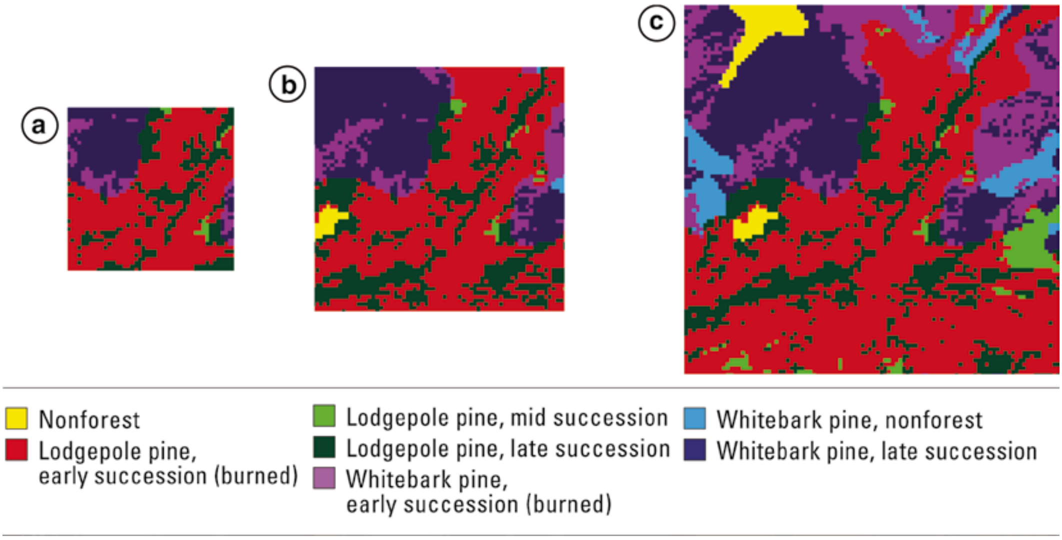

FIGURE 4.8.
Effects of changing extent on a landscape map of southwestern Yellowstone National Park. Note that the presence and relative proportions of the different land cover types change as the extent of the map varies.

dividing a value by area, such as the total length of edge in a landscape vs. an edge density. More sophisticated scaling rules can sometimes be used (e.g., see Wu 2004).

Is there a "rule of thumb" for selecting the appropriate grain and extent for an analysis? Using remotely sensed data for the southeastern USA and examining the effects of changing the grain and extent of the maps on landscape metrics, O'Neill et al. (1996) proposed the following to avoid bias in calculating landscape metrics: The grain size of the map should be 2–5 times smaller than the spatial features being analyzed and map extent should be 2–5 times larger than the largest patches.

#3 A Patch Is Not a Patch

The concept of a "patch" is an intuitive one—we all seem to understand what constitutes a patch of grassland or forest. However, this is yet another example of the need for clear definitions *before* analysis of landscape pattern can begin. Forman and Godron (1986) defined a patch as "…a nonlinear surface area differing in appearance from its surroundings." Converting this definition into a computer algorithm to identify patches on a gridded landscape, we have "…a contiguous group of cells of the same mapped category." But what does contiguous (or touching) mean? Different rules have been established to define this simple concept, and analysis programs usually allow variable patch-definition rules. The two most common methods consider either the four nearest-neighboring cells (i.e., horizontal or

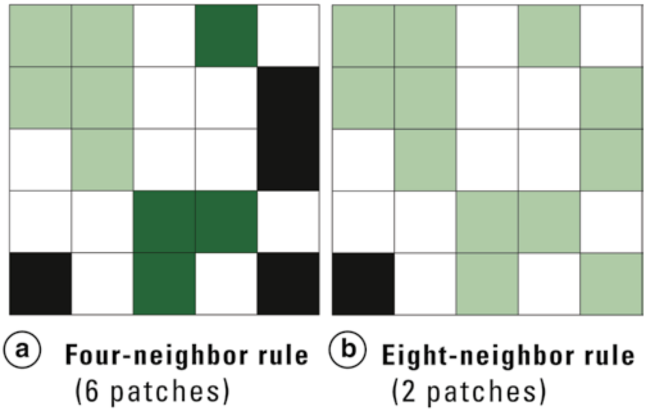

Figure 4.9.
Illustration of the identification of patches (*shaded*) on the same map using either (**a**) a four-neighbor rule, in which the horizontal and vertical neighbors are considered but the diagonal neighbors are not, and (**b**) an eight-neighbor rule, in which the horizontal, vertical, and diagonal neighbors are all considered.

vertical neighbors only) adjoining the cell of interest or the eight nearest-neighboring cells (horizontal, vertical and diagonal neighbors). These different rules produce different results, including numbers of patches, mean patch size, and measures of habitat connectivity (Fig. 4.9). With a four-neighbor rule, there will be more patches of smaller size, and the habitat will appear less connected, compared to an eight-neighbor rule. The four-neighbor rule is conservative, and the eight-neighbor rule seems to be used more widely. The key point is that the user must specify the rule used to identify patches.

Other factors that influence patch analyses also must be considered up front. Patch identification is strongly affected by the grain size and classification scheme of the input data. In general, reducing grain size (i.e., 10-m vs. 100-m cells) will increase the number of patches that are identified because additional detail is resolved at the finer scale. Because classification of cover types or habitats can be very different among species or for different ecological processes, a single map may need to be reclassified to perform patch-based analyses for multiple species or processes. There is also a difference in whether patches are identified *structurally*, based solely on cover type, regardless of whether they are actually used; or *functionally*, in which patches are identified based on differences in expected function (e.g., Fahrig et al. 2011). The same "landscape" may look very different to different species or processes (Li and Reynolds 1993; Fahrig et al. 2011).

In sum, all quantitative analyses that are based on patches (e.g., average patch size, distribution of patches by size, perimeter-to-area relationships, as well as network models derived from graph theory) depend on all of the factors inherent in defining patches. Therefore, the patch-definition process should be well thought out. Patches are not fixed elements of the landscape, but rather are useful spatial constructs that vary with the objectives of a given study.

#4 Many Metrics Are Correlated with One Another (and Thus Redundant)

As with the classification scheme and spatial scale of the data, the metrics chosen for analysis must be selected based on the objectives of the study. However, many metrics are strongly correlated with one another. Correlated metrics are capturing similar qualities of spatial pattern, i.e., they are redundant. As with any other set of variables, care must be exercised to assure that the metrics used in a study reflect the desired quality of spatial pattern, and that they are independent from one another. Failure to account for correlation among landscape predictor variables (such as pattern metrics) can result in incorrect inferences about a response of interest (Eigenbrod et al. 2011a).

The correlation among multiple metrics has been well studied. Multivariate analyses have been informative (e.g., Riitters et al. 1995; Cushman et al. 2008), although resulting interpretations differ in their particulars. Riitters et al. (1995) examined the correlations among 55 different landscape metrics by factor analysis and identified only five independent factors. Thus, many typical landscape metrics are *not* measuring different qualities of spatial pattern. In the Riitters et al. (1995) analysis, the five independent factors represented: (1) the number of classes or cover types on the map; (2) whether the texture of the landscape pattern was fine or coarse; (3) the degree to which patches were compact or dissected; (4) whether patches were linear or planar; and (5) whether patch perimeters were complicated or simple in shape. Thus, the analyst should select metrics that are relatively independent of one another, with each metric (or grouping of metrics) able to detect ecologically meaningful landscape properties. It is usually necessary to have more than one metric to characterize a landscape because there simply isn't one number that "says it all." However, reporting ten highly correlated metrics does not yield new information. Just because something *can* be computed doesn't mean it *should* be computed!

Another issue regarding correlated metrics is that relationships among metrics can be nonlinear. Fortin et al. (2003) explored the spatial realization of simple stochastic processes on a landscape (i.e., using neutral landscape models) and interpreted the resulting patterns using landscape metrics. Inspection of pairwise scatterplots between seven landscape metrics revealed that many relationships were not linear, and several were not even monotonic (Fig. 4.10). Thus, the expectation of linear relationships among landscape metrics that has been implicit in most previous studies may be misleading.

#5 There Is No Single, Magic Metric

Despite wishful thinking and the numerous correlations among landscape metrics, there is not one metric that is sufficient to describe a landscape. How many metrics are needed depends on the key first steps (Box 4.1), which are to define the question and determine what qualities of spatial pattern are of interest. Practically speaking,

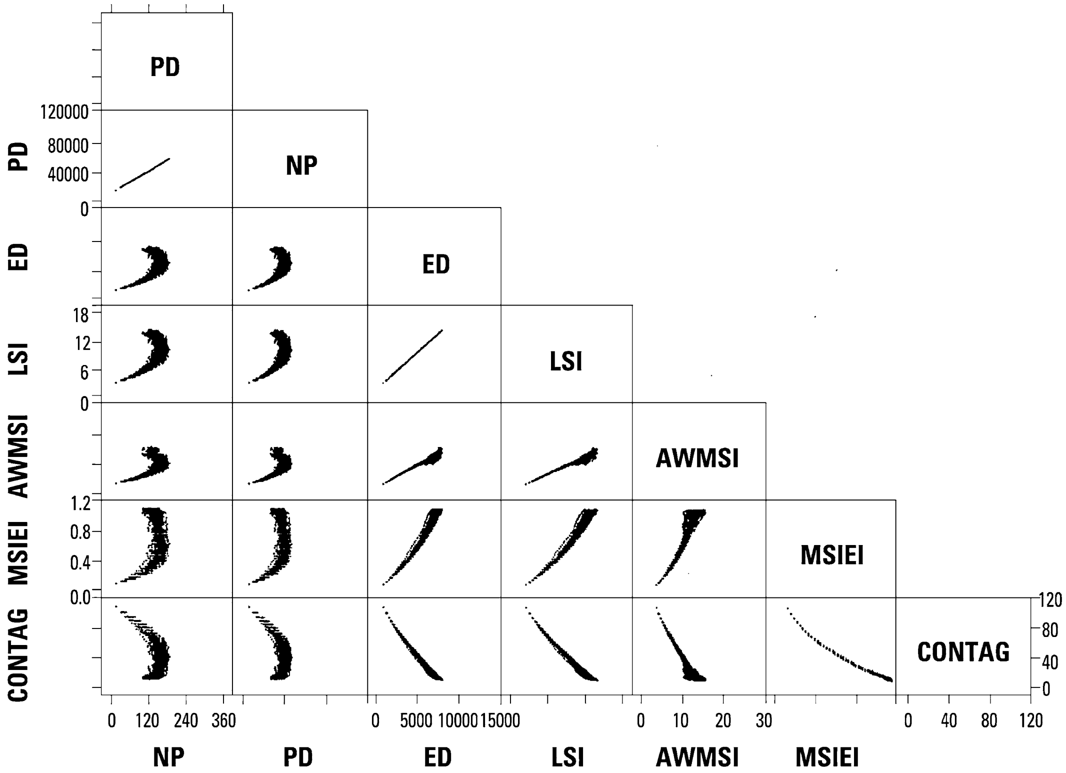

FIGURE 4.10.

Scatter plots of seven landscape metrics derived from 1000 simulated binary landscapes with high autocorrelation. Abbreviations are *NP* number of patches, *PD* patch density, *ED* edge density, *LSI* landscape shape index, *AWMSI* area-weighted mean shape index, *MSIEI* modified Simplson's evenness index, *CONTAG* contagion. The relationships are not monotonic and suggest that relationships among landscape metrics may be nonlinear.

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redundancy should be minimized, and a set of useful metrics must characterize composition and configuration. We re-visit the challenge of making sense out of multiple metrics near the end of the chapter.

METRICS FOR QUANTIFYING LANDSCAPE PATTERN

Caveats thus stated, numerous metrics can be computed for a landscape dataset—too many for us to review in this text. The readings recommended at the end of this chapter provide excellent treatments of the calculation and interpretation of hundreds of metrics. Practical information on several readily available software packages that can be used to analyze landscape pattern is included in Box 4.2. In this section, we review illustrative and commonly used metrics within five broad categories: metrics of landscape composition; measures of spatial configuration, including contagion and patch-based metrics; fractals; surface metrics; and spatial graphs.

Metrics of Landscape Composition

Landscape composition refers to the cover types present on the landscape and how much there is of each class. Metrics of landscape composition are *not* spatially explicit. That is, they measure *what* is present and in what relative amounts, or proportions, without reference to *where* on the landscape they may be located. Metrics of landscape composition are *very* important descriptors, especially because the relative amounts of cover types constrain the potential values of spatially explicit metrics. For example, the proportion of the landscape occupied by a given cover type limits the range of patch number and sizes that are possible (Gardner et al. 1987; see Chap. 3).

Fraction or Proportion (p_i) Occupied

A simple but extremely useful number to calculate is the proportion, p_i, of the landscape that is occupied by each cover type i, where $i=1$, s, and s is the total number of cover types on the map. The p_i values are estimated by counting the number of grid cells of each cover type and then dividing by the total number of grid cells present on the entire landscape. The p_i's have a very strong influence on other aspects of pattern, such as patch size or length of edge in the landscape (Gardner et al. 1987); thus, these proportions are almost always reported. The p_i's are also used to calculate a variety of landscape metrics, contributing to correlations among those metrics sharing this information.

Diversity and Dominance

Metrics based on the relative abundance of each cover type and derived from information theory were first applied to landscape analyses by Romme (1982) to describe changes in the area occupied by forests of varying successional stage through time in a watershed in Yellowstone National Park, Wyoming. Two of these indices are dominance and diversity (O'Neill et al. 1988a), which are inversely related and thus provide the same information about the landscape. Diversity, or relative evenness, refers to how evenly the proportions of cover types are distributed. For example, if there are three cover types present, does each occupy 33 % of the landscape or does one occupy 90 % and the others each only 5 %? The equation for the normalized version of this metric is given by:

$$H = \frac{-\sum_{i=1}^{s} (p_i)\ln(p_i)}{\ln(s)}$$

where H = diversity, p_i = the proportion of the landscape occupied by cover type i, and s = the number of cover types present. Dividing through by ln(s) normalizes the index to range between zero and one. [Other forms of this index that are not normalized have maximum values that depend on the number of cover types and therefore will not scale similarly when the number of cover types vary.] A high value of H indicates greater evenness, and a low value indicates less evenness.

Closely related to diversity is dominance, which is simply the deviation from the maximum possible diversity:

$$D = \frac{H_{\max} + \sum_{i=1}^{s} p_i \ln(p_i)}{H_{\max}}$$

where D = dominance, p_i = the proportion of the landscape occupied by cover type i and $H_{\max} = \ln(s)$, which is the maximum possible diversity for a landscape having s cover types. Again, this index ranges between zero and one with a high value indicating dominance by one or a few cover types, and a low value indicating that the cover types are present in similar proportions. Note that the summation in the numerator actually represents a deviation from $H_{\max}$ because the logarithms of values <1.0 are negative.

Three important points must be noted here. First, H and D are redundant, so an analysis reporting both is of little value. Second, and reflecting a more general issue for metrics of this type, H and D will return similar numerical values for landscapes that have similar proportions of different cover types but are qualitatively different. For example, a landscape occupied by 80 % agriculture, 10 % forest, and 10 % wetland would have the same values of H and D as a landscape occupied by 80 % forest, 10 % agriculture, and 10 % wetland. Thus, these metrics can be difficult to interpret ecologically. Third, these metrics require at least two cover types in the landscape, otherwise the resulting value will be undefined.

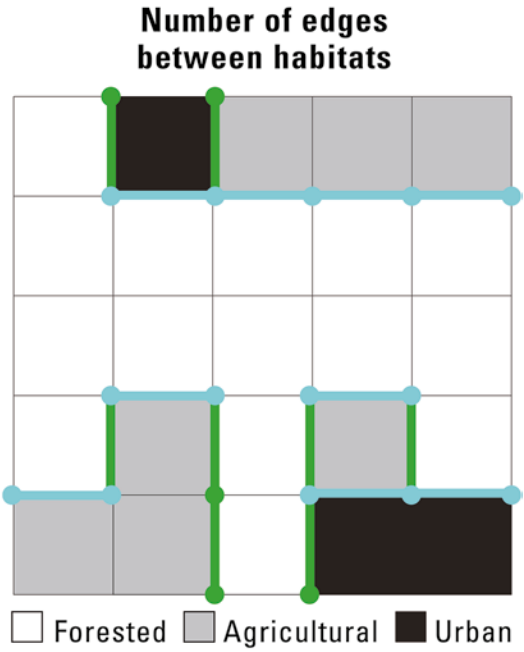
Measures of Spatial Configuration

The metrics described so far do not account for the spatial arrangement of habitat types. Given composition, the metrics of configuration provide quantitative descriptions of the spatial arrangement of cover types on the landscape. These include a wide variety of measures ranging from edge length and edge-to-area ratios; habitat adjacencies and contagion; and the number, size, and distance between patches.

EDGE LENGTH AND EDGE DENSITY

For the overall landscape, total edge is computed by summing the number of horizontal or vertical "edges" between cells of different cover types and reporting that

FIGURE 4.11.
Illustration of how edges are calculated. Map contains three habitats (*black*, *gray*, *white*). The perimeter of the map is usually excluded from edge calculations. In this map, there are nine horizontal edges (*blue*) and eight vertical edges (*green*). Overall edge density can be calculated by summing edge length and dividing by the map area. Assuming 1-ha cells, edge density in this map is calculated by: [(9 + 8) * 100]/25 = 68 m/ha. Edges can also be tallied by cover type.



number, or multiplying by the length units of the cell (Fig. 4.11). The edges along the boundary of the landscape map are usually not included in the calculation. Because the size or shape of landscapes may vary, reporting edge values as a density (length per unit area) is recommended. Because total edge may be difficult to interpret ecologically, it is often more informative to report edge length or density for particular types of edges (e.g., cropland-urban land, or forest-open).

CONTAGION

The contagion metric, C (O'Neill et al. 1988a; Li and Reynolds 1993) uses adjacency information and distinguishes between overall landscape patterns that are clumped or dissected. Like dominance and diversity, the index is derived from information theory, computed from a set of probabilities, and returns a single value that applies to the whole landscape. In this case, however, the values are the *probabilities of adjacency*—i.e., the probability that a grid cell of cover type i is adjacent to a grid cover type j. These probabilities (and thus the contagion index) are thus sensitive to the fine-scale (i.e., cell-to-cell) spatial distribution of cover types. These probabilities of adjacency, $q_{i,j}$, can be computed simply as:

$$q_{i,j} = \frac{n_{i,j}}{n_i}$$

where n_i = the number of grid cells of cover type i and $n_{i,j}$ = the number of instances when cover type i is adjacent to cover type j. Note that this initial calculation assumes a single one-directional pass through the data matrix, i.e., horizontal.

These probabilities can be computed directionally to detect directionality in the pattern (i.e., anisotropy), and average values can also be determined. If you calculate the probabilities simultaneously in four directions, the denominator must be modified to reflect the correct potential number of neighbors.

The set of $q_{i,j}$ values form the Q matrix and provide a lot of information. The $q_{i,i}$ values, which are the diagonals of the Q matrix, are particularly useful in measuring the degree of clumping found in each cover type. The $q_{i,i}$'s give the likelihood that cells of the same cover type are found adjacent to each other. High $q_{i,i}$ values indicate a highly aggregated cover type and low $q_{i,i}$ values indicate that the cover type tends to occur in isolated grid cells or small patches. Thus, this metric can be used to characterize relatively fine-scale detail of the spatial pattern and is useful in providing data on each of the cover types.

The contagion metric, *C*, can be formulated in different ways. By using the elements of the Q matrix as described above (O'Neill et al. 1988a, b), the equation is given by:

$$C = 1 + \frac{\sum_{i=1}^{s}\sum_{j=1}^{s}\left[\left(p_i * q_{ij}\right) * \ln\left(p_i * q_{ij}\right)\right]}{2\ln(s)}$$

Alternatively, a slightly different method of calculating the probabilities of adjacency can be used (Li and Reynolds 1993). Here, the probability of adjacency is given by P_{ij} = the probability that two randomly chosen adjacent pixels belong to cover types *i* and *j*, respectively: i.e., $P_{ij} = P_i P_{j/i}$; and *s* is the number of cover types on the landscape. The equation for *C* is then given by:

$$C = 1 + \frac{\sum_{i=1}^{s}\sum_{j=1}^{s}\left(P_{ij}\right)\ln\left(P_{ij}\right)}{2\ln(s)}$$

The metric ranges from zero to one, with high values indicating more clumped patterns of cover types across the landscape, and low values indicating a landscape with a dispersed or fragmented pattern of cover types. In both cases, the maximum value is dependent on the number of cover types and is given by 2 ln(*s*).

Contagion is useful in capturing fine-scale variation in patterns that relate to the "graininess" of the map. As with *H* and *D*, it is important to know what cover types are present, as the index can return a similar numerical value for landscapes that are functionally very different from one another. However, the index has been demonstrated to be effective at representing overall landscape change (e.g., Proulx and Fahrig 2010). With all of the metrics derived from information theory, it is important to remember that a lot of information is embedded in a single value, and explanations should not neglect composition.

PATCH-BASED METRICS

Given a landscape dataset in which the grid cells are assigned to discrete categories, patches, which are contiguous areas of the same cover type, can be identified and their distributions described. Again, the importance of the classification scheme, scale of the data, and patch-definition rules used in the analysis cannot be overstated! Patch-based measures of pattern include patch number, size, perimeter, and shape.

Patch number, area and perimeter. Once patches are located, the number can be reported, and the area and perimeter of each patch can be computed and summarized. Patch information is most useful when it is reported for individual cover types (i.e., at the class level). It is difficult to interpret values reported for every patch of all cover types in a meaningful way, whereas changes in particular cover types make more sense ecologically. Common ways of reporting patch-level analyses include: a frequency distribution (or cumulative frequency distribution) of numbers of patches by patch size; the number or density of patches; the mean, median, and standard deviation of patch size; or the area-weighted mean patch size. It is useful to report the number of patches as a patch density value (i.e., number of patches divided by landscape area) because that facilitates comparisons among landscapes of different extent.

The frequency distribution of patch sizes on many landscapes is often skewed—a few large patches will be found surrounded by many smaller patches. Under these conditions, the simple arithmetic average does not reflect the "expected" patch size that would be encountered by a simple random placement of points on the map. A more useful method of averaging is to weight patch sizes by area (Stauffer and Aharony 1992). If there are n patches on the landscape and S_k is the size of the kth patch, then the area-weighted average patch size is:

$$S_{\mathrm{a}} = \frac{\sum\left(s_k^2\right)}{\sum\left(s_k\right)}$$

Area weighting of other indices has been employed when skewed frequency distributions result in a disproportionate effect of small patches on the metric of interest (McGarigal and Marks 1995).

Perimeter-to-area ratios (P/A, also referred to as edge-to-area ratios) also serve as useful indices of shape complexity. For a given area, a high P/A ratio indicates a complex or elongated boundary shape and a low P/A ratio indicates a more compact and simple shape. However, P/A is sensitive to patch size, decreasing as patch size increases for a given shape. There are a variety of shape indices based on perimeter and area measurements, some of which correct for the size problem (e.g., see Baker and Cai 1992). If computed separately for each patch in the landscape, the mean, median, standard deviations, and frequency distribution can again summarize these ratios. Note that the P/A values can be reported for particular kinds of habitat adjacencies, and in some calculations, the user can specify the degree of contrast between particular classes.

Two key points about *P/A* calculations bear mentioning. First, the calculation of the mean P/A ratio of *n* patches versus a calculation that uses total length of perimeter in the landscape divided by total area of a cover type are not necessarily the same. Second, remember from geometry class that the relationship of edge to area varies with patch size, even if the shape of the patch remains constant: *P/A* is greater for smaller patches than for larger patches. Area-corrected *P/A* ratios are available.

Largest patch index (LPI), also referred to as the relative size of the largest cluster, is another useful patch-based metric. This is a simple index computed for a given cover type that relates to fragmentation of that cover type. It calculates the size of the largest patch relative to the maximum size possible if the cover type occurred in a single patch:

$$\mathrm{LPI}_i = \frac{\mathrm{LC}_i}{p_i \times m \times n}$$

where LC_i = the size of the largest cluster of habitat type *i*, p_i = the proportion of the landscape occupied by habitat type *i*, and $m \times n$ gives the size of the landscape that contains *m* row and *n* columns. If all of cover type *i* occurs as a single patch, the value of the index = 1.0 indicating complete connectivity. When the cover type is dispersed into very small patches, the index approaches zero. Note that values of LPI are typically correlated with the $q_{i,i}$ values in the **Q** matrix of cell adjacencies.

Patch isolation. The degree to which patches in the landscape are isolated from other patches of the same cover type may be of importance, especially when species habitat-use patterns are of interest. The mean interpatch distance is a measure that relates to the connectivity (or its inverse, fragmentation) of a habitat type. This is often done in one of two ways. First, the distance can be computed from the center of one patch to the center of the next nearest patch. This method requires an algorithm for determining patch centroids. Second, the distance can be computed from the grid cells on each of two patches that are closest to one another, thereby providing a minimum interpatch distance. Although patch distances are usually done for individual cover types, it is also possible to compute these distances between two different cover types, e.g., for an organism that requires two habitats in close proximity.

Proximity index. The proximity index (Gustafson and Parker 1992) is another index that can be computed for each patch on a landscape to determine the relative isolation of the patches. This index is given by:

$$\mathrm{PX}_i = \sum \frac{s_k}{n_k}$$

where PX_i is the proximity index for focal patch *i*, and then within a specified search distance (which must be set by the user), s_k is the area of patch *k* within the search buffer and n_k is the nearest neighbor distance between a grid cell of the focal patch and the nearest grid cell of patch *k*. This index is not normalized but returns an absolute number. Low values indicate patches that are relatively isolated from other patches within the specified buffer distance, and high values indicate patches that are relatively connected to other patches.

Fractals

We consider fractals separately because they may be reported in various ways: overall for the whole landscape, overall for each cover type, or for individual patches. Fractals stirred up a lot of interest because of the promise that they might solve "scaling problems." Although they can be useful in scaling algorithms, their two common uses in landscape ecology have been as measures of shape complexity and as parameters used in generating neutral landscape models. We explain fractals briefly, focusing here on their use as a descriptor of spatial pattern.

Many years ago, the scientist Lewis Fry Richardson studied the relation between the measured length of a coastline or lake perimeter and the scale at which it was mapped. Fry found that the length of the coastline as estimated by the map increased logarithmically with increasing map resolution. Why did this occur? As the resolution of the map was increased, more and more previously unresolved features could be delineated; in the limit, the length of the coastline is infinite. For shapes like coastlines, the curves are never actually as smooth as the drawn lines would have us believe. These findings were incorporated into the theory of fractals proposed by the mathematician Mandelbrot (1983).

The essence of fractals is the recognition that, for many phenomena, the amount of resolvable detail is a function of scale. An important corollary is that increasing the resolution does *not* result in an absolute increase in precision, but rather it reveals variation that had passed unnoticed before. Consider, for example, two ideal fractal curves (Fig. 4.12). If we measure the distance from A to B and measure by units of length x, we observe that in Fig. 4.12a, the distance = 4. If we decrease the resolution by a factor of 3 so units are $x/3 = y$, more detail is seen; in Fig. 4.12b, the distance from A to C is now 4 units of y, but the total distance between A and B will be longer in units of y than in units of x. Because the curves in Fig. 4.12 behave similarly at all scales, once the properties are known at one scale they can be deduced from another merely by applying a scaling parameter. The level of variation present at all scales can be described by a single parameter, the fractal dimension, defined by Mandelbrot (1983) as:

$$D = \log N / \log r$$

where N = number of steps used to measure a pattern unit length and r is the scale ratio. In Fig. 4.12a, b, $N = 4$ and $r = 3$ so $D = 1.2618$.

Mandelbrot (1985) defined a fractal as "a shape made of parts similar to the whole in some way." A fractal will look the same whatever the level of resolution used to observe the object. Fractals have two important characteristics: (1) they embody the idea of *self-similarity*, in which variations at one scale are repeated at another; (2)

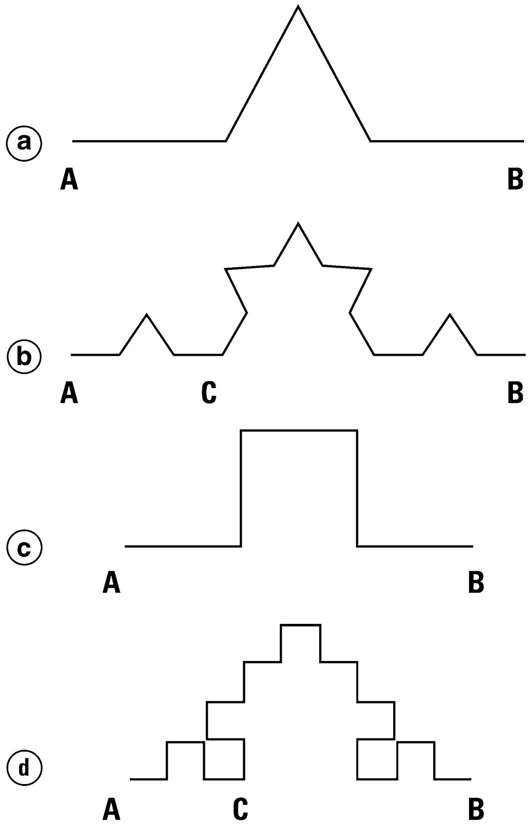
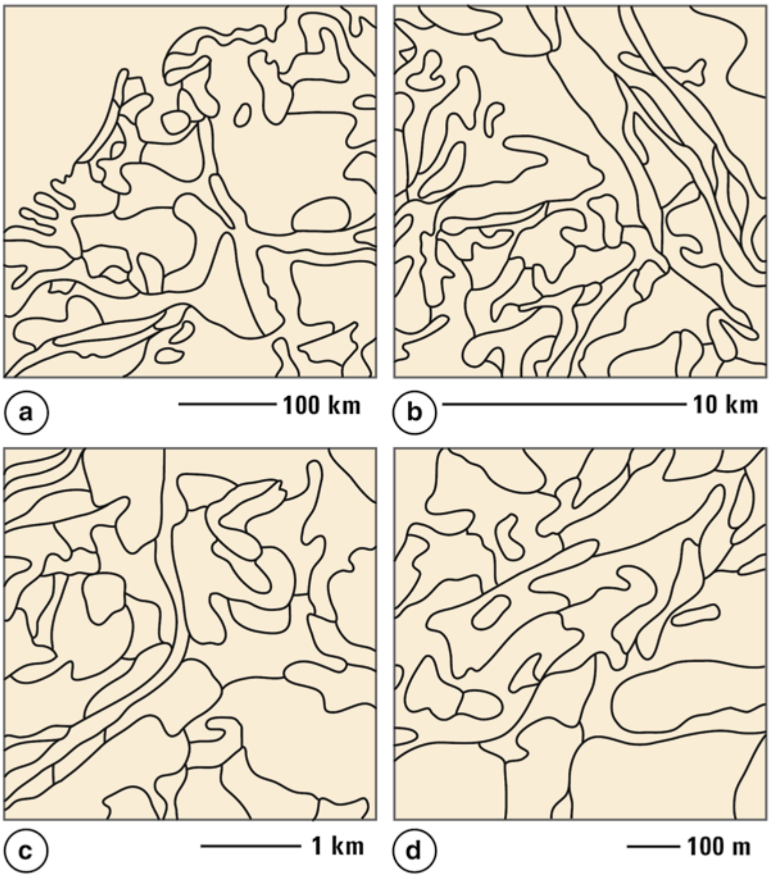


FIGURE 4.12.
Ideal fractal curves: (**a**, **b**) $D = \ln 4 / \ln 3 = 1.2618$; (**c**, **d**) $D = \ln 5 / \ln 3 = 1.4650$. Redrawn from Burroughs (1986).

their dimension is not an integer but rather a fraction—hence the *fractional dimension*, from which these objects acquired the name. Euclidian dimensions are familiar (e.g., a line has a dimension of 1; an area has a dimension of 2; and a volume, such as a sphere or cube, has a dimension of 3.) The value of D for a linear fractal curve can vary between $D = 1$ and $D = 2$. When $D = 1$, it implies that the curve is in fact Euclidian, i.e., a line. As D gets greater than one, it implies that the line has an associated band of "fuzziness" or uncertainty that eats up a little of the second spatial dimension. When $D = 2$, the line has in fact become an area. The concept is easily extended from surfaces to volumes when the value of D ranges between 2 (a completely smooth 2-dimensional surface) and 3 (infinitely crumpled 3-dimensional object).

The idea of self-similarity embodied in the fractal concept implies that if geographical objects such as mountains or rivers are truly fractals, their variations should be scalable. That is, we should be able to predict the patterns at different scales from knowing the pattern at one scale and the fractal dimension. The variation seen in landforms over a few meters, for example, should be statistically similar to that seen over hundreds or thousands of meters when transformed by a simple scaling parameter. The mapped patterns of soils at multiple spatial scale (Burrough 1986) illustrate the way in which this concept might be applied

FIGURE 4.13.
Nested maps of soil patterns in northwest Europe at scales ranging from 100 km (a) to 100 m. (d) Note how natural variation may look similar across scales. Redrawn from Burroughs (1986).



(Fig. 4.13). However, in landscape ecology, their practical application for extrapolating patterns across scales remains limited—but fractals have been extremely useful in generating replicated maps with known spatial structure (see Chap. 3).

Fractal dimensions also have been used as a metric of the complexity of landscape patterns. For example, Krummel et al. (1987) found that forest patches showed a distinct change in fractal dimension, with smaller patches having a simpler shape than larger patches (Fig. 4.14). The reason appears to be that small patches were woodlots whose boundary was affected by human management; the large patches were more complex because they tended to follow natural boundaries, such as topography. A number of other studies have also found lower fractal dimensions in human-dominated landscapes or cover types (e.g., Turner 1990; Mladenoff et al. 1993). While the fractal dimension has been useful in these studies, the same result can often be obtained with simpler metrics, such as edge-to-area relationships.

Measures of Landscape Texture

The metrics described thus far require classification of landscape data into discrete categories. Because these metrics have been used so widely, much of our current

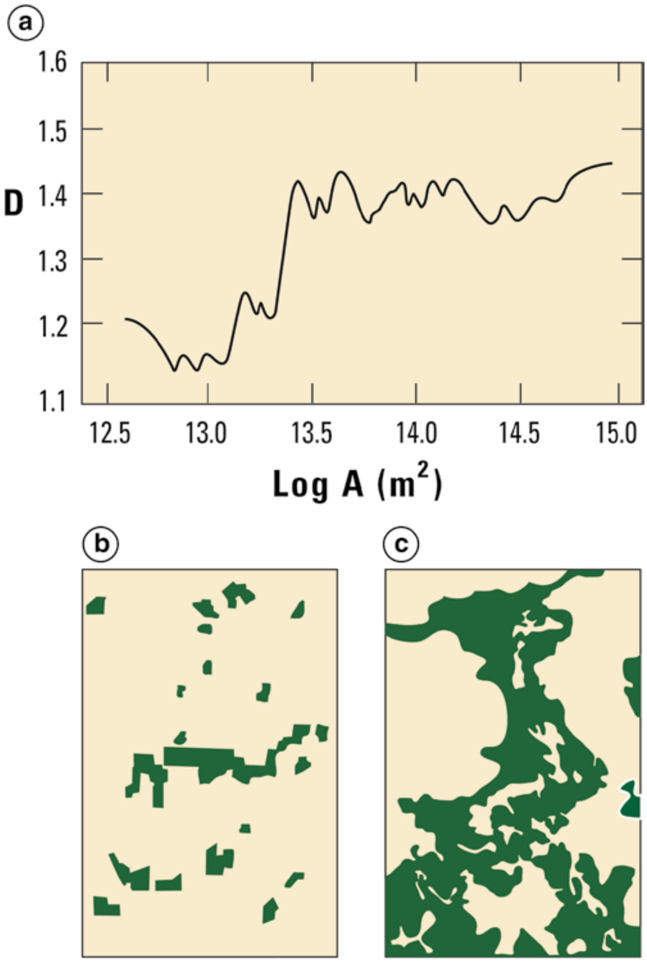


FIGURE 4.14.
(**a**) Fractal dimension (*D*) of forest patches in the vicinity of Natchez, Mississippi as a function of patch size. (**b**) Section of the original map illustrating how small patches tend to be simple in shape. (**c**) Section of the original map illustrating the more complex shapes associated with the larger patches. Redrawn from Krummel et al. (1987).

understanding of pattern-process relationships is derived from categorical representations of spatial heterogeneity. If landscape data are continuous rather than categorical, quantitative approaches that do not require the data to be categorized might be desirable. Such approaches include spatial statistics, which are covered in the next chapter, as well as a suite of methods that quantify the texture or surface characteristics of continuous data (McGarigal et al. 2009). Some of these approaches were introduced early in landscape ecology (e.g., image texture methods were suggested as landscape indices by Musick and Grover 1991), but the conceptual simplicity and intuitive appeal of metrics based on categorical data contributed to their widespread use (McGarigal et al. 2009).

To explore the potential of metrics based on continuous data to capture unique aspects of spatial pattern, McGarigal et al. (2009) presented 17 metrics that characterize surface topology and applied them to a sample of landscapes. They also created categorical maps for each sample landscape, computed a set of the standard metrics and compared the two groups of results. A clustering analysis was conducted to determine how these metrics separated out. One group of surface metrics related to the overall surface diversity, analogous to edge density and contrast; the other groups did not correlate strongly to any of the categorical metrics, indicating that they may quantify different qualities of pattern. Attributes of surface topology that are measured by the metrics include surface roughness, the shape of the surface height distribution, angular texture, and radial texture (McGarigal et al. 2009). These metrics are intriguing, and their inclusion in the current version of FRAGSTATS means that many users can investigate their behavior. Their potential for generating new insights about pattern-process relationships in actual landscape ecology studies remains to be determined.

Measures of Landscape Connectivity

A complementary approach to the metrics discussed thus far focuses on measures of connectivity (Tischendorf and Fahrig 2000; Calabrese and Fagan 2004; Fall et al. 2007; Kindlmann and Burel 2008). In some landscapes, cell-based approaches are not good models for spatial structure, and alternative approaches (e.g., dendritic networks, Grant et al. 2007; road density, Heilman et al. 2002) may be used. When habitats become fragmented, the degree to which organisms can move among habitat patches becomes increasingly important. The importance of connectivity in conservation and reserve design has fostered a proliferation of connectivity metrics (Kindlmann and Burel 2008). Although its influence on population dynamics and genetic diversity is recognized, definitions of connectivity have been inconsistent. Connectivity can be defined structurally, based on habitat patterns and assumptions about organism dispersal, or functionally, based on where organisms actually move. Connectivity also can be considered a property of the entire landscape or of a particular habitat patch (Calabrese and Fagan 2004). We consider connectivity as the degree to which the landscape facilitates or impedes movement of organisms.

As noted by Calabrese and Fagan (2004), connectivity metrics come in a variety of flavors. Nearest-neighbor approaches are used widely and easy to calculate, but they do not perform well (Moilanen and Nieminen 2002). Patch connectivity metrics incorporate the number of patches or area of habitat within some radius of the patch, such as the proximity index described previously, may be indicators of connectivity. Such metrics depend on the radius, or buffer distance, selected by the analyst. It is advisable to distinguish between landscape connectivity and patch connectivity.

Spatial Graphs and Network Analyses

Another set of connectivity metrics derives from graph theory (Urban and Keitt 2001; Fall et al. 2007; Minor and Urban 2008). These approaches represent pattern across a landscape as a series of nodes (points, which typically represent habitat patches) and links (connections among the points). Landscape graphs can be used to examine patterns of connectivity, identify potential pathways for dispersal or movement, and prioritize patches for conservation. The approach was recognized early in landscape ecology: Forman and Godron (1986) suggested the Gamma index as a useful measure:

$$\gamma = \frac{L}{L\max} = \frac{L}{3(V-2)}$$

where L = the number of links in the network and V = the number of nodes in the network. This index can range between zero to one with low values indicating less connectivity and high values indicating higher connectivity.

Recent years have seen a considerable advancement in the types and sophistication of metrics that characterize connectivity based on the properties of a network. There is a whole lexicon for network analyses (Table 4.3) related to the number of nodes, the number of links, and the degree to which nodes are connected directly or indirectly (i.e., through longer paths) with other nodes. Nodes also may be weighted by characteristics such as area or habitat quality to better represent their importance for habitat connectivity in the landscape. Of particular interest in landscape ecology applications are metrics that characterize how the properties of a component or the overall network change when particular nodes or links are removed or added.

A suite of metrics have been developed by Saura and colleagues to assess habitat connectivity that incorporate the effects of habitat connectivity and area into a single metric (Fig. 4.15). The Integral Index of Connectivity (IIC, Pasqual-Hortal and Saura 2006) and Equivalent Connected Area (ECA(IIC), Saura et al. 2011) both do so. For example, consider the ECA(IIC) index:

$$\mathrm{ECA}(\mathrm{IIC}) = \sqrt{\sum_{i=1}^{n}\sum_{j=1}^{n}\frac{a_i \cdot a_j}{1+nl_{ij}}}$$

where n is the total number of patches in the landscape; a_i and a_j are the areas of patches i and j, respectively, and nl_{ij} is the number of links in the shortest path between patches i and j. The units of this index are area (e.g., ha, m^2), and the index ranges between the size of the smallest and largest patches on the landscape. The maximum possible value occurs when all habitat is found in a single patch. This metric weights the nodes by their area, and other formulations incorporate weighting of the links based on the likelihood of dispersal (Saura et al. 2011). These metrics are widely used for conservation applications in Europe.

Network metrics rooted in graph theory nicely complement those that are based on categorical maps, but their statistical and ecological limitations must still be understood. The definition of what constitutes "habitat" (i.e., the way in which the landscape has been categorized for a given study) still has a fundamental effect on the numerical answers. However, potential limitations and biases in metrics derived from graph theory are not well recognized (Kupfer 2012). Research targeted toward understanding the behavior of these metrics at a level comparable to

Table 4.3.
Terms and connectivity metrics derived from network theory (modified from Lookingbill and Minor 2015; also see Fall et al. 2007).

Term	Definition
Network analysis terms	
Nodes	Points or vertices representing habitat patches
Links or edges	Lines that connect nodes
Component	Groups of nodes (patches) that are connected to one another by links
Hub	A node that has many links
Isolated node	A node that has few or no links
Path	For a sequence of connected nodes, a walk in which no node or link is visited twice
Path length	The shortest distance between two nodes
Landscape-level metrics	
Area of largest component (ALC)	Proportion of habitat that is contained within the largest component; calculated by dividing habitat area in the largest component, H_{LC}, by total habitat, H_T; only patches above a minimum size appropriate for the organisms of interest are considered
Link density	Number of links (L) in the network divided by the maximum number of links, given by $L/[n(n-1)/2]$, where n = number of nodes in the network. Reported as a proportion
Patch-level metrics	
Degree centrality	Total number of links that connect to a given node; also called node degree; this measures local connectivity, as it accounts for nearest neighbors only, but can be reported as an average for all nodes
Domain	Total number of nodes that are reachable, through the network, from a given node; this measures larger-scale connectivity of patches because it extends beyond the immediate direct connections

what has been learned about more traditional landscape metrics (e.g., from studies using neutral landscape models) would be informative. Further, empirical studies that compare the relative effectiveness of alternative representations of landscape patterns in relating to landscape functions are still needed (Kupfer 2012).

Social Network Models

Statistical models developed for social networks appear promising for incorporating actual movement into network models (Fletcher et al. 2011). Most spatial network analyses have been based on the landscape structure and assumptions

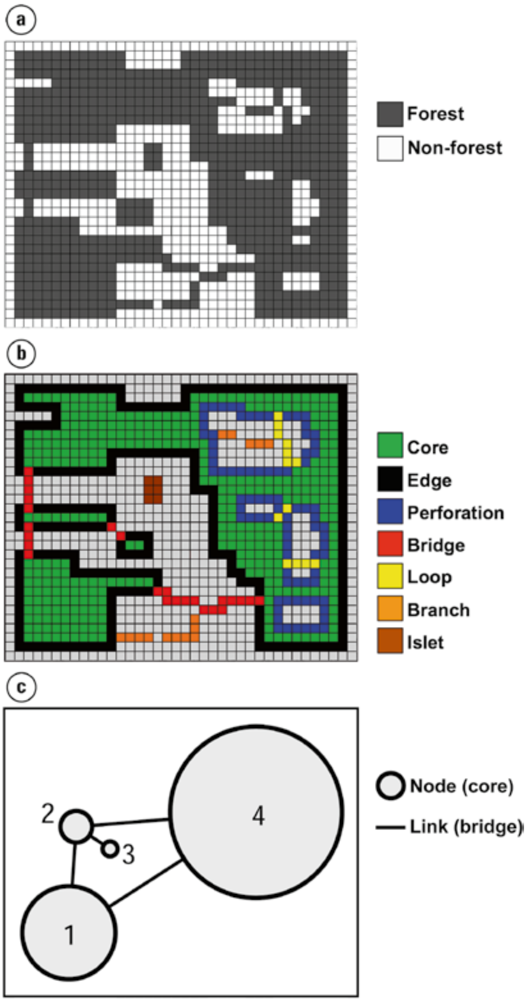


FIGURE 4.15.
A three-step process that converts the initial patch structure of a forested landscape (**a**) into a network of links and nodes (**c**); see Vogt et al. (2007) for the methods and software used to identify the different elements of map structure and connectivity labeled in (**b**). Figure adapted from Saura et al. (2011).

about movement among resource patches. For example, links in the network are assumed connected if the nodes (patches) are within the maximum known dispersal distance or dispersal kernels (Fletcher et al. 2012). Direct tests of whether network analyses provide meaningful estimates of actual movements (i.e., functional connectivity) are few. However, Fletcher et al. (2012)) sampled actual movement among patches for two different species (*Chelinidea vittiger*, a cactus-feeding insect; and a bird, *Rostrhamus sociabilis plumbeus*, the endangered Everglades Snail Kite), then tested the ability of network models to represent landscape connectivity. The network model based on maximum movement distance consistently had the lowest accuracy in predicting linkages and consistently over-predicted connectivity. Two kernel-based constructions were moderate in predictive accuracy, and the social network models that also accounted for directionality in movements were generally best at predicting linkages (Fletcher et al. 2012; Fig. 4.16). An important take-home message from this study is that the way in

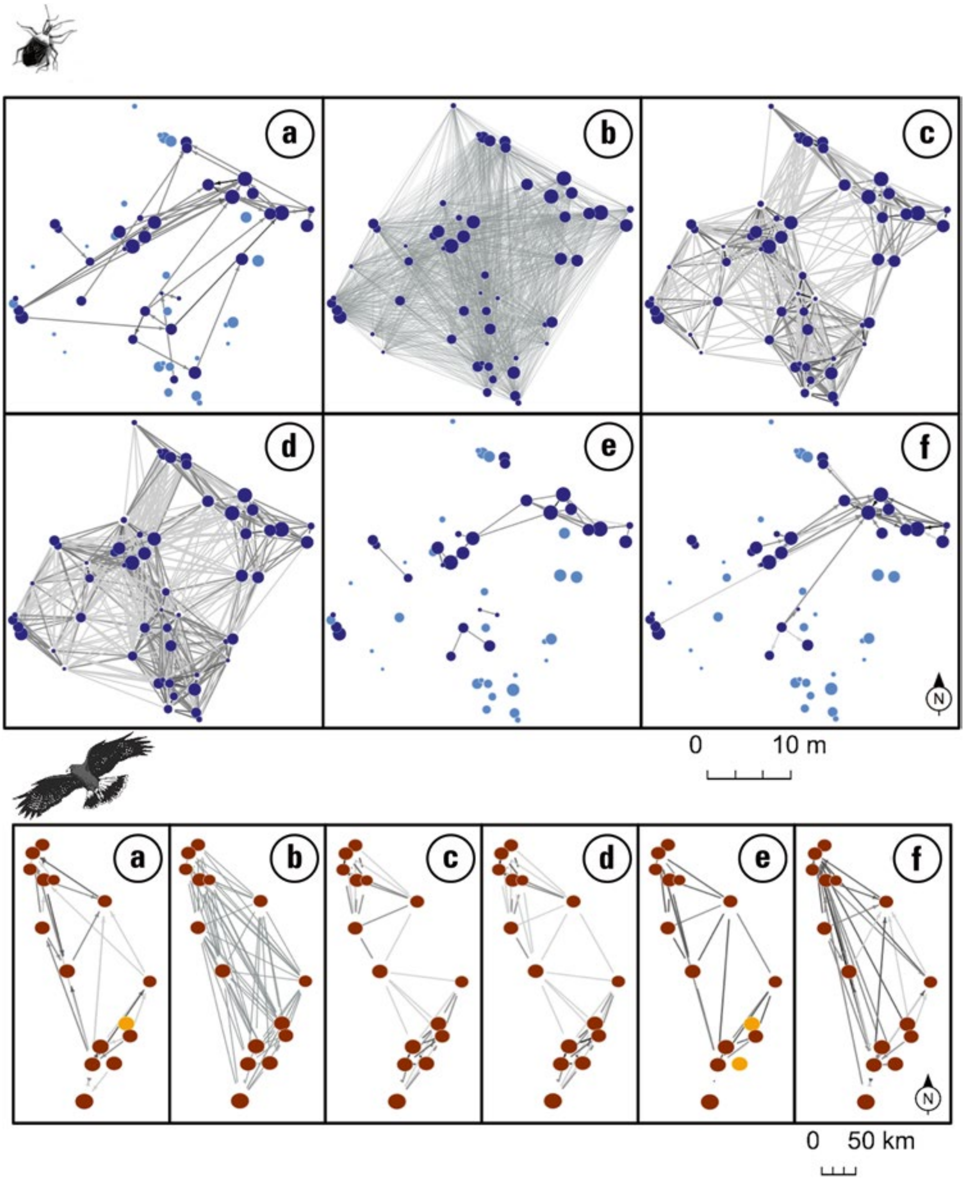


Figure 4.16.

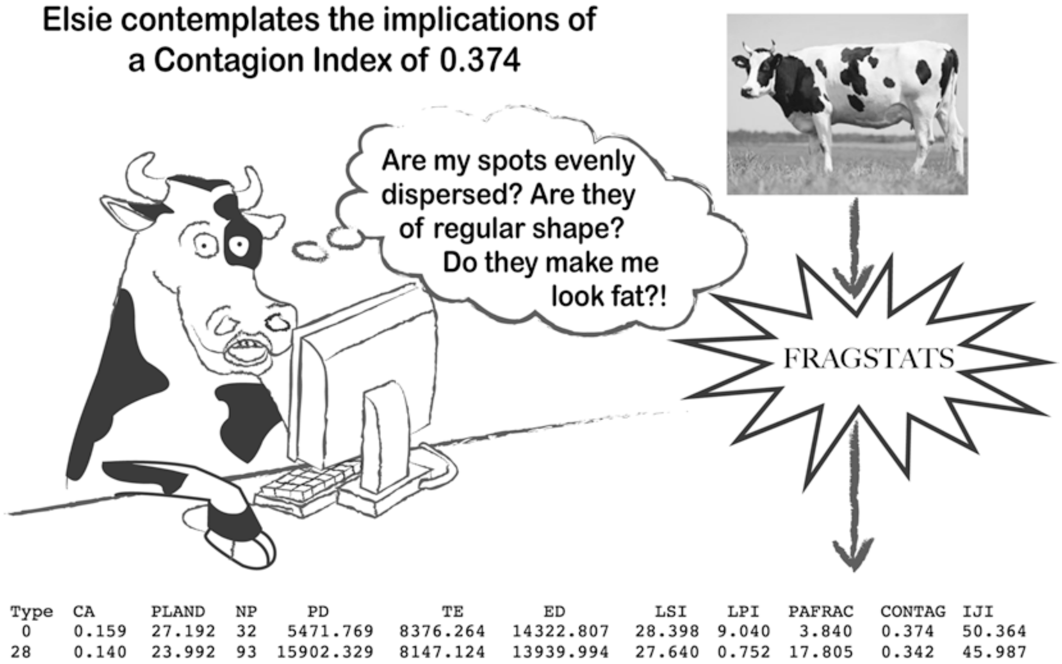
Alternative networks of landscape connectivity for within-field movements of *Chelinidea vitiger* (a cactus-feeding insect; *upper*) and breeding-season movements of *Rostrhamus sociabilis plumbeus* (Everglades Snail Kite, *lower*) across wetlands in Florida, USA. (**a**) The observed network, (**b**) the maximum observed distance moved, (**c**) theoretical kernel, (**d**) empirical kernel, (**e**) latent space, and (**f**) sender–receiver constructions for each species. Node size is proportional to log(patch size), and gray scale of links denotes intensity of observed and predicted movements. Light-colored nodes are habitat patches that are not connected to other patches.

Reproduced with permission from Fletcher et al. (2012).

which a network is constructed profoundly influences the resulting network and the inferences regarding landscape connectivity. Understanding potential vs. actual landscape connectivity remains a research frontier.

LANDSCAPE METRICS: WHAT IS THE STATE OF THE SCIENCE?

Since the review by Gustafson (1998) and the first edition of this book, the tools for analyzing landscape pattern have become well established, the behavior of most metrics is well understood, and landscape metrics are widely used. Landscape ecologists face no paucity of ways to quantify innumerable aspects of spatial pattern, and the number of metrics can be overwhelming (Fig. 4.17); we often kiddingly advocate for a moratorium on new metrics! Recent advancements also have contributed to increased rigor landscape pattern analyses, and we focus here on two



```
Type  CA     PLAND   NP    PD         TE        ED         LSI    LPI    PAFRAC  CONTAG  IJI
 0    0.159  27.192  32   5471.769   8376.264  14322.807  28.398 9.040   3.840  0.374   50.364
28    0.140  23.992  93  15902.329   8147.124  13939.994  27.640 0.752  17.805  0.342   45.987
```

FIGURE 4.17.

Landscape metrics are now widely used, but interpretation can still be tricky. The purpose of any landscape-pattern analysis is what makes pattern metrics informative and useful. Users must understand the range, behavior, and meaning of any metric that is used in a study (cartoon adapted from Kupfer 2012).

key areas: evaluating significant differences in landscape patterns and interpreting multiple metrics. We then discuss the use of metrics as landscape indicators and conclude with some practical advice and recommendations.

What Constitutes a "Significant" Difference in Landscape Pattern?

A long-standing challenge in landscape ecology has been ascribing statistical significance to differences in landscape metrics either through time or among landscapes. In cases where a single number is reported for a landscape (e.g., a patch density or value of contagion), we often have little understanding of the degree to which landscape pattern must change to detect an ecologically important or statistically significant change in the numerical value of the metric (Wickham et al. 1997). This has led to a variety of challenges in studies that compare landscapes (e.g., is a Dominance value of 0.75 different from 0.80?), and some erroneous conclusions (e.g., inferring a landscape has become more fragmented when *C* declines from 0.88 to 0.86). In statistical analyses of empirical data, significance is typically assessed by estimating the variance among replicate samples. In landscape ecology, replication is challenging at the very least, and oftentimes impossible. Early comparisons among landscapes were limited because metric distributions were poorly known, and expected values and variances were not available for statistical comparisons and hypothesis testing (Remmel and Csillag 2003; Li and Wu 2004).

Recent advances provide practical ways of assessing differences in landscape metrics. Remmel and Csillag (2003) used neutral landscape models based on composition and configuration to assess the statistical properties of six widely used landscape metrics (number of patches, patch density, edge density, landscape shape index, area-weighted mean shape index, and contagion). They generated 1000 replicate landscapes for different habitat proportions and levels of spatial autocorrelation and analyzed these maps using FRAGSTATS. The results were used to describe the sensitivity of the metrics to composition and configuration, as done in previous studies, and to examine the nature of the relationship between metric pairs. Correlations were nonlinear for several pairs of metrics and strongly influenced by p (Fig. 4.10). However, the replication also allowed the authors to generate confidence intervals around expected values for each landscape metric, which permits statistical comparisons to be made.

Remmel and Csillag (2003) next compared the pattern of forest cover in four sample landscapes surrounding Prince George, Canada (Fig. 4.18) and used the confidence intervals for making robust inference about differences. They first estimated composition and configuration parameters (i.e., class proportion and spatial autocorrelation) from each of the four images (see Fortin et al. 2003) and used those parameters to simulate 1000 landscape realizations based on each pair of parameters. Each landscape replicate was analyzed in FRAGSTATS, and they com-

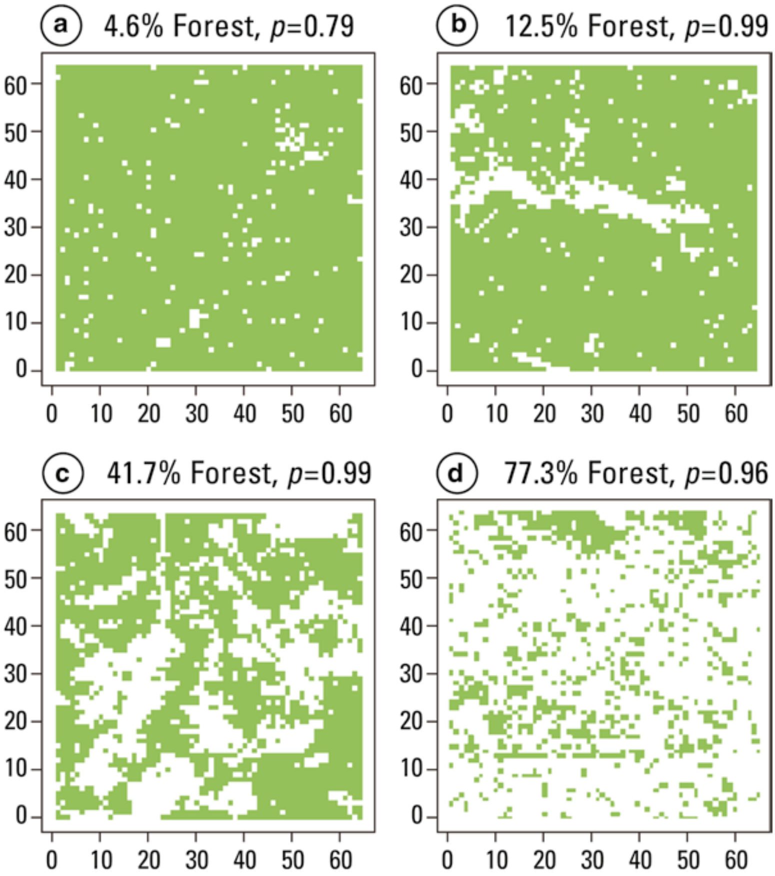


FIGURE 4.18.

Four forested landscapes from Prince George, Columbia, Canada with percent forest cover ranging from 4.6 (a) to 77.3 % (d). Forests are indicated in white while nonforested areas are shaded. Landscapes a through d correspond to those plotted in Figure 4.19. Pixel resolution is 30 m.

ADAPTED FROM REMMEL AND CSILLAG (2003).

puted the expected value and 95 % confidence interval for each metric. If the confidence intervals for a given metric overlapped between two landscapes, then the landscapes did not differ for that metric (Fig. 4.19). This approach lends much greater rigor to studies that seek to identify differences among landscapes or to detect changes through time in a given landscape, and methods for generating and analyzing neutral landscape models are readily available. Understanding of the statistical properties and behavior of many pattern metrics has improved, and best practices for appropriate statistical comparisons should become standard in landscape ecology.

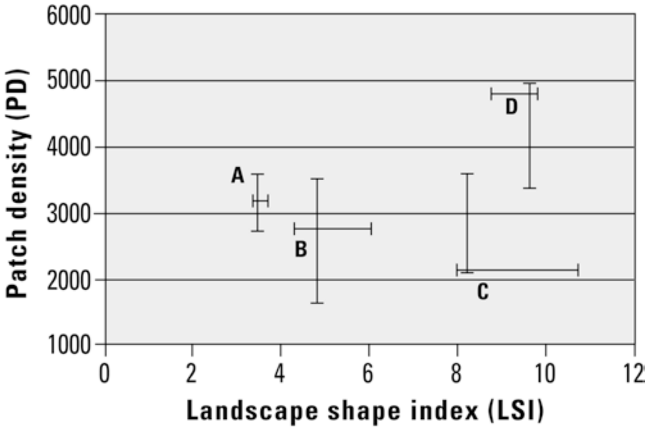


FIGURE 4.19.
The 99 % statistical confidence intervals for measures of patch density and landscape shape index for four landscapes (*A*–*D* in Fig. 4.18) near Prince George, British Columbia, Canada. Solid circles are actual values measured from each landscape, and confidence intervals are derived from 100 realized simulations. Patch density did not differ significantly among the landscapes, but landscape shape index discriminated landscapes *A*, *B*, and *C*–*D*.

REPRODUCED WITH PERMISSION FROM REMMEL AND CSILLAG (2003).

Making Sense Out of Multiple Metrics

The description of landscape pattern does require more than one metric, so the question becomes how to select a relevant subset. Determining how many metrics to use and how to combine the metrics so that the results are meaningful and interpretable is not a trivial task. Several recommendations can serve as a guide. First, as we have emphasized repeatedly, metrics must be chosen to answer a particular question or objectives; reporting the whole "kitchen sink" is to be avoided. Second, the subset should explain pattern variability across the landscape, but redundancy should be minimized. Thus, metrics should be relatively independent of one another. Third, the measured values of the metric should extend over a substantial portion of the range of potential values. The analyst must know the potential range of the metric as well as how much of that range is represented in the study landscapes. If the metric does a poor job of detecting the differences in pattern and varies little, the metric will not be useful. Using only a portion of the potential range of a metric used as a predictor variable in a landscape study is a known pitfall that can lead to erroneous conclusions (Eigenbrod et al. 2011a).

STATE-SPACE METHODS

One method of combining information from multiple measures is to plot the values in a state space defined by a few independent metrics that capture different qualities of pattern that are relevant to the original question. For example, if one was quantifying a landscape and how it changed through time from the perspective of a particular animal, one might be interested in (1) the proportion of the landscape containing suitable habitat, (2) the number of patches of suitable habitat above the minimum size required by the animal, and (3) the connectivity of the suitable habitat as measured by interpatch distances. The condition of the landscape could be plotted through a 3-dimensional state space based on the coordinates of each of the three metrics considered. Furthermore, the volume within that state space that represented the zone of survival for the animal could be identified. One could then determine whether or not particular landscape changes result in a landscape trajectory that remains within or takes excursions beyond that zone of survival. Such an analysis could be done in *n* dimensions, though the visualization and interpretation will become increasingly complicated. What is particularly powerful about this approach is that the structure of a landscape can be plotted through time or compared to a desirable state, and the Euclidian distance between points quantified. Both direction and magnitude of change through time can be plotted if repeated measurements are made for the same landscape.

O'Neill et al. (1996) used a 3-dimensional "pattern space" to show three subregions of the southeastern USA as points characterized by landscape indices (Fig. 4.20). Use of the pattern space effectively separated these landscapes based on dominance, contagion, and shape complexity. Simple geometry can be used to compute the distance between landscapes in the pattern space. O'Neill et al. (1996) described two important constraints on this approach. First, the axes of the pattern space should as orthogonal, i.e., as independent from each other, as possible. Simple correlation analysis can be used to test for independence. Second, the sensitivity of the individual metrics used in the pattern space to landscape change must be established. The critical question is whether the indicator can detect small changes (i.e.,

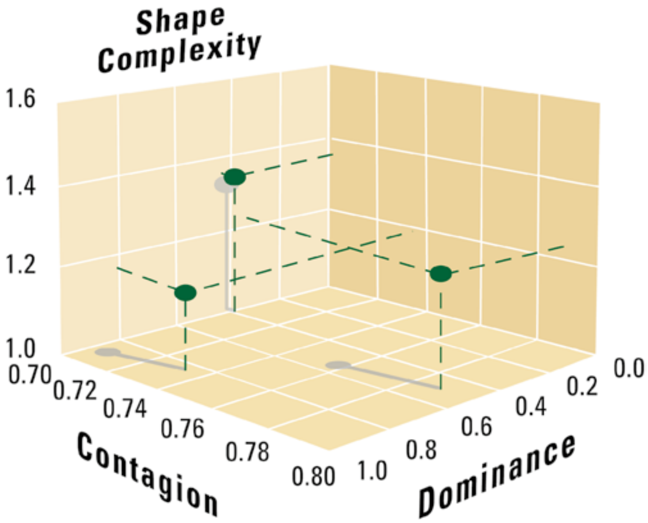


FIGURE 4.20.
Three-dimensional "pattern space" in which three subregions of the southeastern USA are characterized by three landscape metrics.

ADAPTED FROM O'NEILL ET AL. (1996).

changes that are not catastrophic or irreversible) such that it serves as a useful warning of undesirable landscape change (O'Neill et al. 1996).

MULTIVARIATE ANALYSES

Multivariate statistics also offer a means of making sense out of multiple metrics. Riitters et al. (1995) compared 55 landscape metrics across 85 land-cover datasets. Pairwise comparisons revealed that many metrics have correlation coefficients greater than ± 0.9. Eliminating the redundant measures reduced the candidates to 26. Factor analysis revealed five factors that all had eigenvalues greater than 1.0 and explained about 83 % of the variance. Each factor contained several metrics. Based on the ease of calculation and interpretation, the following relatively independent metrics were recommended: (1) the total number of different land cover types on the map; (2) contagion, (3) fractal dimension, (4) average patch perimeter-area ratio, and (5) relative patch area (average ratio of patch area to the area of an enclosing circle), which indicates how compact the patches are. These five metrics provided a minimum set of independent measures of qualitatively different aspects of spatial pattern based on 85 landscapes scattered across the USA.

Other studies have suggested subsets of measurements that might characterize landscape pattern. McGarigal and Marks (1995) also conducted a principle components analysis of 30 different metrics calculated for late-successional forests in the northwestern USA. Their analysis revealed three independent factors: (1) patch shape and edge contrast, (2) patch density, and (3) patch size. Li and Reynolds (1994, 1995) used theoretical considerations to propose five different aspects of spatial heterogeneity that could be computed: (1) number of land-cover types; (2) proportion of each type on the landscape; (3) spatial arrangement of patches; (4) patch shape; and (5) contrast between neighboring patches. One would then select a metric to quantify each of these fundamentally different aspects of pattern to avoid redundancy among metrics. Hargis et al. (1998) found contagion and edge density were inversely correlated, but measures of interpatch distances were not highly correlated with other metrics.

The lack of concordance among multivariate analyses of landscape metrics prompted a recent study by Cushman et al. (2008). These authors used PCA on landscape metrics computed for multiple landscapes (>150) in each of three geographically isolated regions to identify independent components of landscape structure and to determine whether these were idiosyncratic or common across regions. In other words, are results differing among studies simply because different regions, or landscapes, have characteristic differences in pattern? They evaluated the strength of each component using thee measures: universality, strength, and consistency (Cushman et al. 2008). *Universality* was defined as the percentage of classes or regions in which a component is found. *Strength* assessed the average variance explained by a structure component across classes and regions. *Consistency* measured the stability of component interpretation among classes and regions. The analyses suggested seven

TABLE 4.4.
HIGHLY UNIVERSAL AND CONSISTENT CLASS-LEVEL AND LANDSCAPE-LEVEL METRICS DERIVED FROM ANALYSIS OF 531 LANDSCAPES ACROSS THREE DIFFERENT REGIONS IN NORTH AMERICA (BASED ON CUSHMAN ET AL. 2008).

Component name	Description
Class-level metrics	
Edge contrast	Degree of "contrast," or the magnitude of difference in some feature, between focal class and its neighborhood (user defined)
Patch shape complexity	Shape complexity based on perimeter-area relationships defining focal patch shape
Aggregation	Degree and aggregation of cells of the focal class, where large, compact clusters are considered to be aggregated
Nearest neighbor distance	Proximity of patches of the focal class, based on average (or area-weighted average) distance between nearest neighbors
Patch dispersion	Spatial arrangement of patches across the landscape, from clumped to random to uniform, based on variability in nearest-neighbor differences
Large patch dominance	Degree of concentration of focal class area in few, large patches with large core areas
Neighborhood similarity	Relative isolation of focal patches from neighboring patches of the same class
Landscape structure metrics	
Contagion/diversity	Relative aggregation and diversity, respectively, of all cover types within the landscape
Large patch dominance	Relative measure of landscape dominance by large patches
Interspersion/juxtaposition	Relative intermixing of cover types
Edge contrast	Degree contrast among cover types, where contrast is user defined and represents the magnitude of difference among classes in one or more attributes
Patch shape variability	Variability in user-defined perimeter-area metrics
Proximity	Relative isolation of patches from nearby patches of the same class
Nearest-neighbor distance	Area-weighted average distance between patches of the same cover type

SEE TEXT FOR ADDITIONAL EXPLANATION.

class-level components of landscape structure that were highly universal and consistent, and seven landscape-level components that were highly universal (Table 4.4). These results suggest that there are consistent combinations of landscape metrics that universally describe landscape patterns.

Although covariance among landscape metrics is often considered to be a "problem" in landscape analyses, it can also be informative and used to advantage. In their multivariate analysis of landscape patterns across the conterminous USA, Cardille and Lambois (2010) used the 1992 NLCD dataset to analyze >190,000 contiguous sample landscapes (each 6.48 km × 6.48 km) that covered the entire 8-million-km^2 area. A total of 1921 landscape and class-level metrics were calculated for each landscape and stored on the publicly available METALAND server (Cardille et al. 2005). From this large set of metrics, a PCA was used to identify a set of independent axes, and then the similarity values among pairs of sample landscapes were computed. An affinity propagation algorithm identified 17 distinct clusters of landscapes based on their patterns of land use and land cover and a single "exemplar" that best represented that cluster. A striking result from this analysis was the ubiquitous human signature observed on landscapes of the conterminous USA (Cardille and Lambois 2010). The authors also noted that the total information content of landscape metrics is what enabled the objective classification of different kinds of landscape.

Metrics and Landscape Indicators

While the pros and cons of different metrics will be debated long into the future, there remains interest in using metrics as indicators of how landscapes are changing over time and what this may mean for the environment. The selection of individual metrics that act as indicators of spatial pattern and presumably relate to some aspects of ecological function (e.g., Jones et al. 2001; Gergel et al. 2002) is another way in which a landscape metrics can be used. Such landscape-indicator metrics measure structural heterogeneity—that is, the metrics are computed on the land-cover classes without a direct and explicit relationship to ecological processes. They can be especially useful for monitoring change over time and space, much as other aspects of the environment (e.g., temperature, water quality, water flow) receive routine monitoring. Ideally, indicators should be transparent, easy to understand by scientists and nonscientists alike, and easy to calculate.

As part of its 2008 STATE OF THE NATION'S ECOSYSTEMS, the Heinz Center (2008) proposed a set of eight landscape indicators, each with a well-developed scientific rationale, for tracking change across the USA. The indicators were meant to evaluate landscape structure through a lens that would ideally capture some aspects of ecosystem function by answering: how much are is occupied by each ecosystem or land-cover type? What are the shapes and sizes of patches of an ecosystem type, and how are they intermingled with one another? The indicators include some of the metrics we have described above (e.g., several include patch-based measures), and they also include variables such as housing density and distance of a particular land-cover type from residential development (Table 4.5). The Heinz Center (2008) report nicely addresses the question of why land managers or

TABLE 4.5.
SUGGESTED LANDSCAPE INDICATORS CHARACTERIZING CHANGE OF DIVERSE LAND-USE TYPES OVER TIME ACROSS THE USA (MODIFIED FROM HEINZ CENTER 2008).

Landscape indicators	
System	Indicator
Core National	Selected suite of pattern metrics for "natural" lands (lands relatively unaffected by human activities)
Coasts and oceans	Selected suite of pattern metrics defining landscapes of coastal areas
Farmlands	Measures of the relative proximity of croplands to residences; relative frequency of patches of "natural" lands within agricultural landscapes
Forests	Suite of pattern metrics characterizing forested landscapes
Fresh waters	Measures of natural in-stream continuity and connectivity
Grasslands and shrublands	Suite of pattern metrics characterizing grassland–shrubland landscapes
Urban and suburban landscapes	Housing density changes; relative frequency of patches of "natural" lands within residential and urban landscapes

policy makers would care about tracking each indicator, and it serves as an example of how landscape pattern analyses can make important contributions to environmental policy.

Some Additional Practical Advice and Parting Words

Methods and metrics for quantification of spatial pattern on categorical maps abound. We have discussed a number of basic calculations here but have not attempted to present all metrics that have been proposed. Metrics will come and go, but study design is key, regardless of what metrics you use for an analysis. Known pitfalls should be avoided (e.g., Eigenbrod et al. 2011a, b), and carefully considering the questions provided in Box 4.1 can help you to steer clear of traps. Readers interested in gaining practical experience in computing metrics and becoming familiar with some of the widely used software programs can also consult Gergel and Turner (2016).

It is important to remember that metrics of composition and configuration are intertwined, even in the simplest landscapes. An early paper by Gustafson and Parker (1992) illustrated this nicely, showing how a variety of metrics change in interesting (and predictable) ways with habitat abundance. Given this tight relationship, under what conditions does spatial configuration matter? How much explanatory or predictive power does configuration add to composition? Understanding the relative importance of landscape composition vs. spatial configuration is important in any study and remains a key question in many pattern-process relationships. When using landscape metrics in addressing this question, you must know what aspects of landscape pattern you are trying to quantify and why. The question, "when does spatial pattern matter?" continues to be open and interesting.

As a landscape ecologist, do not try to publish everything that can be computed—be selective and strategic. Be wary of complicated metrics; many studies have shown that simple metrics that are easy to interpret can be as (or more) powerful than metrics that require many intermediate steps (Haines-Young and Chopping 1996; Li and Wu 2004). Parsimony is a virtue! Furthermore, metrics computed for individual cover types are often easier to interpret than if the values are computed for the whole landscape. It is difficult to figure out why single numbers are changing if the number comes from all cover types across the whole landscape, and ecological meaning often requires more information (what kind of patches increased or decreased?) Also be careful when comparing results for metrics that require decisions or parameters set by the used (e.g., edge contrast, core area, proximity index).

Interpreting landscape metrics ecologically and ascribing significance to them remains tricky. Landscape pattern analyses are often based on the implicit (and usually untested) assumption that the pattern metric(s) directly relates to the process of interest. The distinction between structural and functional heterogeneity (or connectivity) recognized this difference (Li and Reynolds 1995; Fahrig et al. 2011), but it bears repeating. As we will see throughout the rest of this book, landscape ecologists have made tremendous progress in building the library of empirical studies that provide empirical linkages between pattern and process.

SUMMARY

The quantification of landscape pattern is necessary for understanding the effects of pattern on ecological processes and for documenting either temporal changes in a landscape or differences between two or more landscapes. Numerous metrics are used by landscape ecologists to quantify landscape patterns, and readily available data and analysis software has made such analyses routine. Different groups of metrics used with categorical data characterize landscape composition (i.e., what cover types are present and in what relative abundance) and configuration (i.e., how are the cover types spatially arranged). Metrics derived from graph theory provide quantitative estimates of habitat connectivity at the patch and landscape level. One major limitation of overall metrics of pattern, i.e., those reported for a whole landscape rather than by cover type, is that the same numerical value can be returned for a variety of qualitatively different landscapes.

One metric is insufficient to characterize a landscape, yet there is no standard recipe for determining how many and which ones are needed. A useful set of metrics to quantify landscape pattern should meet several criteria, including: (1) the metrics should be selected to answer a particular question or meet a particular objective; (2) the measured values of the metrics should be distributed over the full range of potential values and the behavior of the metrics should be known; (3) the metrics should be relatively independent of each other. Independence can (and should always) be tested by examining the correlation structure among a set of potential candidate metrics. In addition, the analyst must recognize (and carefully choose) the classification scheme used to categorize the data, the spatial scale of the data and any user-defined rules (e.g., patch definition). This set of decisions, along with the accuracy of the spatial data, places important constraints on the analysis and interpretation of landscape pattern. As a first approximation, the extent of the study landscape should be 2–5 times larger than landscape patches to avoid bias in calculating landscape metrics; grain size should be 2–5 times smaller than the spatial features of interest.

The development of landscape pattern analysis has been rapid, but metrics used with categorical data have stabilized and their statistical properties and behavior are better known. Advancements in landscape analyses methods have led to improved understanding of how suites of metrics related to one another and more robust methods for making statistical comparisons among landscapes. Ongoing research continues to address the relative sensitivity of different metrics to detecting changes in the landscape and to better document the empirical relationships between landscape patterns and ecological processes of interest. Continued progress will help landscape ecologists determine what is worth measuring and why, and when a change in a metric is significant both statistically and ecologically.

DISCUSSION QUESTIONS

1. Imagine that two landscapes have been analyzed by a series of metrics, and a number of differences have been detected. What assurances regarding the reliability and usefulness of the data should be examined *before* conclusions are drawn about differences between the two landscapes?
2. Classification of landscape data is required for most spatial metrics. How will alternative classifications affect the analysis of pattern? Using a landscape dataset of your choice, design an experiment to test the effect of classification schemes on analysis results.
3. Imagine that you are charged with designing the protocol for monitoring change through time in a large region (you should select a region on which to focus). Describe the steps you would take to develop your monitoring scheme. How would you select the metrics to be included? Distinguish between "inventory" metrics (what's there and

what it looks like) versus hypothesis-testing metrics (e.g., pattern change which may affect or respond to an important ecological process in your region).

4. Compare and contrast traditional landscape metrics based on categorical data and connectivity metrics derived from graph theory. Are these methods capable of answer the same scientific questions? In what ways are they similar or different in terms of data availability and sensitivity to data accuracy?

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C H A P T E R 5

SPATIAL STATISTICS

In contrast to land-cover or habitat classes, some kinds of landscape data are recorded as continuous numbers rather than discrete categories. Such data include vegetation density or height; net aboveground primary production; nutrient mineralization rates; percent of biomass killed by a disturbance; and distances from lakes, roads, or other features of interest. Most landscape metrics covered in Chap. 4 are not appropriate for quantifying the spatial pattern of continuous variables, and a different set of methods is required. Spatial statistics, including *geostatistics*, are used to quantify the spatial structure of continuous data, and they are widely applied in landscape ecology. Spatial statistics and geostatistics use point data for some property that is spatially distributed across the landscape; they do not require categorization of the landscape nor do they assume a patchy structure or the presence of boundaries. Observations, conventionally labeled as z, are made at specific x, y locations and referred to as *regionalized variables* (Palmer and McGlinn 2016). Spatial statistics then quantify *spatial dependence* in the regionalized variable, or the tendency of z measured at one x, y location to be correlated with, or depend on, values of z measured at another x, y location. If there is spatial dependence in z, then information about z at one place allows you to infer information about z at another place. Spatial statistics quantify the magnitude of variance in the data, the proportion of that variance that is spatially dependent (i.e., spatially autocorrelated), and the scales, or distances, over which variables are spatially dependent. These methods are powerful, but the terminology and methods can be daunting for those new to the subject.

Landscape metrics and spatial statistics are distinct but complementary methods of analysis. Gustafson (1998) illustrated this point nicely by considering two

M.G. Turner, R.H. Gardner, *Landscape Ecology in Theory and Practice*,
DOI 10.1007/978-1-4939-2794-4_5

different ways of describing the spatial distribution of aspen (*Populus tremuloides*), a widely distributed tree species in North America. If one converts measurements of aspen tree density to categorical data by delineating patches where aspen is present above some minimum density threshold, the resulting map of aspen distribution can be analyzed using patch-based metrics. Alternatively, if one uses the actual measures (continuous numbers) of aspen density at locations throughout the landscape, then the spatial structure of aspen density would be analyzed using spatial statistics. Both approaches characterize the spatial pattern of aspen on the landscape, but they do so in different ways. Quantifying patterns of disturbance in a landscape offers another example (Fig. 5.1). Areas in a landscape affected by fire can be categorized as discrete patches of burned vs. unburned areas (Fig. 5.1b) and analyzed using landscape metrics, or represented by continuous measures of fire severity (Fig. 5.1a) and analyzed using spatial statistics (see Turner and Simard 2016). Both approaches assess the spatial structure of fire effects on the landscape, but they allow different forms of analysis and inference.

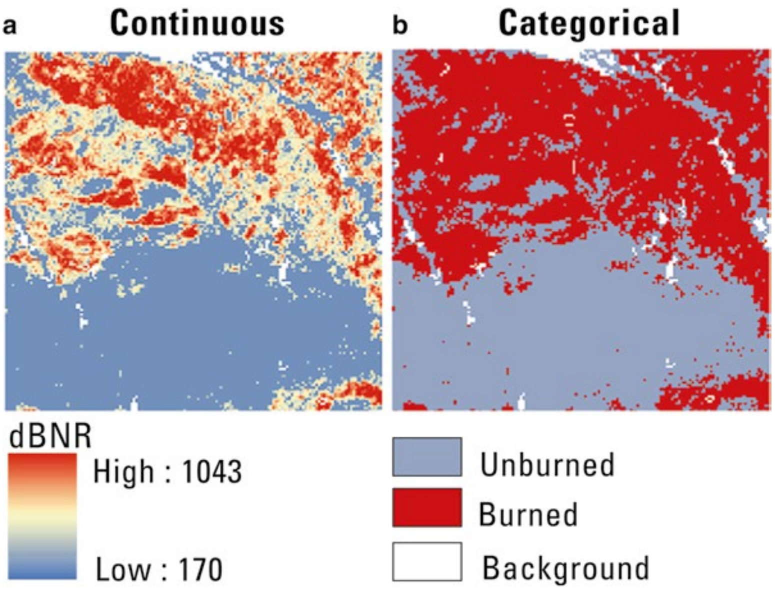


FIGURE 5.1.

Example of two ways to depict fire patterns in a 5 km × 5 km area of the Greater Yellowstone Ecosystem, Wyoming, USA. The left map shows continuous estimates of fire severity based on the Differenced Normalized Burn Ratio, with warmer colors indicating higher fire severity. The right map classifies these data into burned vs. unburned cells. Although both depict fire patterns, these maps would be analyzed with different methods.

MAPS GENERATED BY MARTIN SIMARD.

The origin of spatial statistics is often traced to the South African mining engineer, D. W. Krige, who developed methods for locating ores within geologic formations and for whom the spatial interpolation method of *kriging* is named. In the 1950s, Krige pioneered statistical methods to predict the location of economically valuable ores (e.g., gold, uranium) using a limited number of boreholes. This work spurred development of methods for spatial evaluation of mineral resources based on geographically referenced point measurements and led to the field of geostatistics. These methods still provide a basis for *spatial interpolation*, which uses measurements at particular points to predict values in locations that lack empirical measurements and is discussed in detail below.

We begin this chapter by explaining several key uses of spatial statistics in landscape ecology, present important caveats for their use, and then provide a brief overview of major approaches. The literature regarding spatial statistics is large, diverse, and technical (Law et al. 2009), making a complete review well beyond the scope of this text (see Legendre and Legendre 1998; Fortin and Dale 2005 for broad coverage of spatial statistics). Our goal is to demystify the elementary jargon of spatial statistics and to provide illustrative examples emphasizing how these methods can be used in landscape ecology. We do this by focusing on two techniques that have been widely applied and that illustrate the general principles (and pitfalls) of the use and application of spatial statistics in landscape ecology. These two methods are (1) point pattern analysis, which analyzes observed "events" (e.g., nest locations, fire starts, etc.) and (2) spatial autocorrelation and variography, which use many spatially distributed measurements of continuous variables. We conclude the section on variography with a short discussion of efficient sampling designs that reduce the cost of acquiring sufficient data for using spatial statistics in landscape studies. But first, let's think about why these methods are useful and note key caveats to consider and pitfalls that may be encountered. The methods themselves are rapidly evolving as spatial data and analysis software become more available; therefore, as we did for landscape metrics, we first emphasize general considerations that should apply to most problems of landscape analysis.

WHY DO LANDSCAPE ECOLOGISTS USE SPATIAL STATISTICS?

The use of spatial statistics in ecology has become widespread and much more sophisticated since the first edition of this book, and access to computation software has increased. Why have these methods become so important, and why are they used in landscape ecology?

Spatial Independence

As encapsulated in Tobler's first law of geography: "Everything is related to everything else, but near things are more related than distant things" (Tobler 1970). However, independence among data values is one of the most common assumptions of standard parametric statistics. As Tobler's law suggests, when data are collected within a spatial framework, values near one another are often correlated; this violates the assumption of independence and complicates data analysis (Ripley 2005). What is the primary statistical danger? When measurements are spatially autocorrelated (i.e., near things are related to each other, so the data are not independent), there is an increased risk of Type I error—finding a statistically significant difference when none actually exists (i.e., erroneous rejection of the null hypothesis). A simple example illustrates this problem. Imagine a transect along which measurements of plant height are made, and you wish to determine whether the mean plant height is 20 cm. Assume that the variance is known and equal to 5, and you calculated a mean height of 21.5 cm from ten measurements made at 3-m intervals along the transect. A computed Z statistic will reject the null hypothesis with $p = 0.034$, leading you to conclude that the measured mean plant height differs from 20 cm. Now assume that the adjacent sampling points were not independent, but rather they were correlated with $r = 0.40$ (i.e., spatially dependent). A correction to the Z test yields $p = 0.14$, leading to the opposite conclusion that plant heights are not significantly different from 20 cm. Thus, spatial dependence in the data can cause the conclusions of a statistical analysis to change qualitatively. An important application of spatial statistics in landscape ecology is to determine the magnitude and scale of spatial dependence and to adjust either the sampling design or the statistical models to account for this lack of independence.

The plant-height example is a simple one, but spatial autocorrelation in landscape data is the rule rather than the exception. From a practical standpoint, reviewers of proposals or manuscripts routinely expect authors to have tested for spatial dependence and to have adjusted the analysis for spatial effects by using appropriate statistical methods and associated tests. When pilot data are available, spatial statistics can be used to describe the change in dependence with distance between samples and, from this analysis, set a separation distance beyond which measurements are spatially independent. This distance defines the minimal spacing required for future sampling locations that will allow the assumption of independence among measured values to be valid. For example, Pearson et al. (1995) used spatial statistics (semivariograms) to determine the scale over which measurements of winter grazing intensity by elk (*Cervus elaphus*) were spatially dependent, then subsampled data at distances beyond that scale to assure independent samples for analysis of how grazing intensity varied with environmental characteristics. When the degree of spatial autocorrelation in a dataset is not known a priori, spatial dependence can be evaluated in the raw data or from the residuals of a statistical analysis. When spatial autocorrelation is detected in the residuals, the statistical model must be adjusted to account for this dependency (see Legendre 1993; Fortin and Payette 2002; Ishihama et al. 2010).

Even when it may not have been welcomed, detection of spatial dependence can be a source of new insights about a focal variable. Spatial dependence in the residuals of a statistical model should alert the investigator to the potential importance of a spatial process that was not previously considered. For example, Anderson et al. (2013) examined the spatial distribution of a nonnative invasive plant across a large mountainous landscape. After accounting for the local and landscape-level variables that predicted presence of the invasive plant, spatial dependence was still present in the residuals up to a scale of 3 km. The residual spatial structure suggested a hierarchical process of invasion. The spatial pattern was consistent with infrequent, long-distance dispersal events resulting in new nascent subpopulations that subsequently spread via shorter-distance dispersal (Anderson et al. 2013). Thus, residual spatial autocorrelation, after accounting for other covariates, can be informative and not simply problematic.

Nature of Spatial Structure

Spatial statistics are also used in landscape ecology when an explicit goal is to understand the nature of the spatial structure of a particular variable, or set of variables, and to test hypotheses about that spatial structure. Quantifying variability in ecological measures over space (and time) is complementary to estimating average values or central tendency (e.g., Benedetti-Cecchi 2003; Fraterrigo and Rusak 2008). Variability can be highly sensitive and capture effects that are obscured by averaging. Although variance estimates are used less frequently than categorical landscape metrics for hypothesis testing in landscape ecology, use of measures of spatial variation are increasing (Legendre et al. 2002, 2004). For example, spatial statistics have been widely used to evaluate hypotheses about how disturbances or land-use history alter the magnitude or scale of variability in an ecological response (e.g., Gross et al. 1995; Lane and BassiriRad 2005; Mayor et al. 2007; De Jager and Pastor 2009, among others). For instance, Fraterrigo et al. (2005) found that historic agriculture in the Southern Appalachian Mountains was associated with altered spatial variability in soil resources, even though average soil variables were comparable with undisturbed areas. Soil resources varied over very fine spatial scales in undisturbed forests, but that spatial variability was homogenized in forests with historical land use such that soil resources were correlated over broader spatial scales (Fraterrigo et al. 2005). The magnitude and scale of spatial dependence in one variable also may be used as predictors for another variable, as illustrated by Gundale et al. (2006), who hypothesized that the spatial structure of variability in soil nitrogen would predict plant responses.

Spatial Interpolation

Another use of spatial statistics in landscape ecology is spatial interpolation. Some variables simply cannot be measured everywhere, yet we may wish to estimate values at locations that were not sampled and/or produce a continuous surface, or map, of expected values. If the spatial structure of response variables is known, information about their autocorrelation can be used to predict their expected values at unmeasured locations—as Krige did to predict the likely locations of ore deposits. Landscape ecologists have developed spatial interpolations for a wide range of phenomena and scales. Bolstad et al. (1998) used kriging (among other methods) to predict vegetation patterns in a 2185-ha forested landscape in the Southern Appalachians. Smithwick et al. (2012) used kriging at much finer scales, predicting postfire rates of net nitrogen mineralization, abundance, and composition of soil microbes and aboveground vegetation within four 0.25-ha plots in Greater Yellowstone (USA) from point measurements (Fig. 5.2).

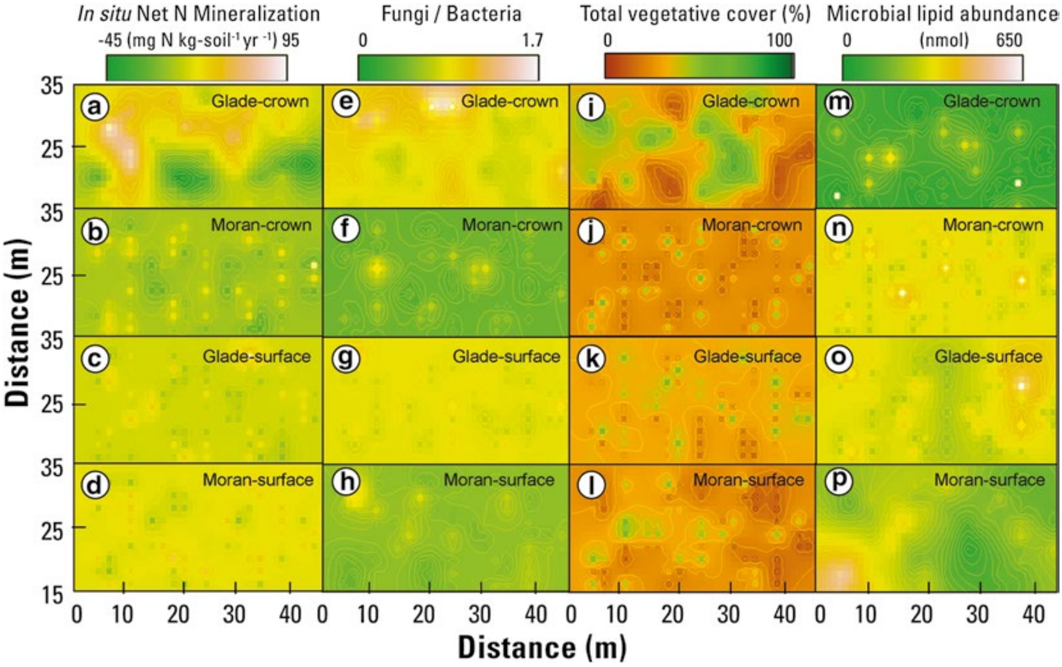


FIGURE 5.2.

Kriged maps of (**a**–**d**) in situ net nitrogen mineralization rate, (**e**–**h**) fungi:bacteria ratio, (**i**–**l**) total vegetative cover, and (**m**–**p**) microbial lipid abundance in four postfire study plots in Greater Yellowstone. Data were sampled at points, and semivariogram analysis was used for spatial interpolation.

FROM SMITHWICK ET AL. (2012).

Thus, in landscape ecology, spatial statistics provides important quantitative analysis tools to appropriately analyze continuous spatial data and to test new hypothesis regarding the magnitude, scale, and patterns evident in these data. Consequently, knowledge and use of spatial statistics are essential for studying pattern-process relationships in landscape ecology.

CAVEATS FOR USING SPATIAL STATISTICS, OR "READ THIS FIRST"

As we did for landscape metrics in Chap. 4, we begin by providing guidance about what to consider *before* embarking on an analysis using spatial statistics. As always, it is critical that the question or rationale for analysis be clearly specified at the outset. The importance of beginning with a good scientific question can never be overstated!

#1. The Spatial Dependence in Landscape Data Must Be Characterized and Considered

The need to recognize and test for spatial autocorrelation in data may be the most important take-home message from this chapter. The advances in spatial statistics and the understanding of how spatial dependence can affect conclusions drawn from data require a "heads-up" approach to this issue. Data recorded at intervals along transects and/or grids, especially along topographic or other environmental gradients, will often display spatial dependence over considerable distances (e.g., Everson and Boucher 1998; Nelson et al. 2005). In fact, it is difficult to imagine any landscape data that will not display spatial dependencies at some scale. As we showed with the simple example of plant heights, failure to characterize these dependencies can lead to serious biases in analysis and incorrect conclusions. It is incumbent upon the scientist to realize that spatial dependence is a potential issue, to appropriately test the data or models for spatial dependence, and to adjust the analysis accordingly. Such data exploration should be a routine component of statistical analyses, just like examination of other estimates of model strength and goodness of fit. If there is no spatial dependence, there should be a sentence in the manuscript stating that conclusion (e.g., Simard et al. 2012 do this). The old adage, "ignorance of the law is no excuse," will apply; be assured that reviewers and editors will follow up.

#2. Spatial Autocorrelation Is Not Always a Problem

Although spatial autocorrelation is often considered a nuisance that interferes with testing interesting relationships between predictors and response, it is important to recognize that spatial dependence can provide ecologically relevant information.

Changes or differences in the spatial scale of autocorrelation can indicate changes or differences in the processes that have generated the observed patterns. Early spatially explicit studies of soils demonstrated that nutrient pools and transformations varied tremendously over small distances (e.g., Robertson et al. 1988), and that spatial variability could change through time (Gross et al. 1995; Cain et al. 1999). A study of postfire succession and soils illustrates hypothesis testing using spatial dependence as a response. Turner et al. (2011) asked how the variability and structure of aboveground vegetative cover and soil nitrogen availability changed during the first 4 years following stand-replacing fire. They laid out a set of expectations that could be tested with spatial data. For example, they expected little initial spatial structure in soil nitrogen variables because fire effects were likely to be spatially random, but that spatial structure would develop with vegetation recovery during early postfire succession (Turner et al. 2011). Results revealed a surprising absence of spatial structure in soil nitrogen transformations at the scales sampled. For biotic cover, the scale of autocorrelation was expected to increase over time, but it remained similar during the first 4 years postfire.

Nested scales of variability can suggest that the environmental factors structuring variability operate at different scales (e.g., Franklin and Mills 2003). Processes that homogenize local variation at a particular scale can induce spatial autocorrelation that then emerges at coarser scales (as shown by Fraterrigo et al. 2005). Furthermore, the spatial scale over which two variables are correlated may indicate an underlying process that is worth exploring. For example, analyses by Keitt and Urban (2005) using *wavelets* showed how topographic variation in physical drivers (e.g., sunlight, water availability) interacted to produce complex, scale-dependent patterns in vegetation growth (Keitt and Urban 2005). In short, the analysis of spatial data by autocorrelation methods can provide important insights into the spatial structure of both response and driver variables.

#3. Coincidence of Scales of Spatial Dependence Among Multiple Variables Does Not Prove Causality

The coincidence of scales of variability of different ecological features, such as plants and soil nutrients (Grieg-Smith 1979) or seabirds and their prey (Schneider and Platt 1986) may indicate linkages worth exploring. However, it is important to remember that coincidence of the spatial structure does *not* prove causality, but rather suggests reason to test for causal mechanisms. As is always true when correlations exist among variables, statistical dependencies imply but do not prove pattern-process dependencies. In applying spatial statistics, it is tempting to surmise that variables having similar spatial structure may be responding to similar processes or that the variables may interact with one another. Here, the art of analysis will be instrumental for relating a coincidence of scales to potential mechanistic relationships.

#4. Scale Always Matters

The grain and extent of the data used in spatial statistics will influence the results, much as they influence landscape metrics. For continuous data, *grain* is usually the minimum or characteristic distance between sample points, whereas *extent* refers to the total area sampled, typically the linear dimension defining the sampled area. The characteristic distance between the points must be equal to or less than the scale at which the analyst wants to detect spatial structure. The overall linear extent of the dataset should be at least twice the maximum distance the analyst wishes to examine. Thus, to explore spatial dependence over scales of 1–100 m, sampling points should be separated by ≤ 1 m, and the overall data dimension should be at least 200 m. In general, fine-grained spatial structure cannot be determined from coarse-grained data, and broad-scale patterns cannot be adequately detected with data of limited spatial extent.

As for patch-based metrics, boundary effects are an important consideration when determining scale-dependent effects. All landscapes are of finite size and, because of this, edge effects dominate estimates derived from data that lie near boundaries. When these boundaries are artificial and the landscape is relatively small, truncation effects occur and may dominate estimates. Because these truncation effects are especially serious for point pattern analysis (discussed below), special correction factors may be required. Many of the scale issues associated with data collection can be reduced or eliminated if an optimal sampling plan can be devised ahead of time. Fortin and Dale (2005:14) provide guidance for developing landscape sampling designs, and we discuss some approaches later in the chapter. The purpose should be to obtain a match between the goal of the study, the spatial and temporal grain and extent of the data, and the validity of the statistical methods to be used for analysis.

Practically speaking, it is critical to check the analysis scales used when computing spatial statistics, especially when using readily available software. For ease of computation and display, software programs may automatically "bin" the data into 10–20 classes representing different separation distances among the data points. If the extent of the data is large, the characteristic bin sizes will also be large and may fully contain smaller separation distances that may be ecologically relevant. The unsuspecting analyst might obtain results using overly large bins that obscure, rather than detect, the finer-scaled variation. Therefore, the analyst must know the finest resolution needed for the analysis and the maximum separation distance that should be considered, then confirm these settings before results are determined. The bottom line is that you must carefully select the scales needed for data collection and analysis, then fit the models accordingly.

#5. Stationarity Is an Important Assumption in Many Spatial Statistical Analyses

The assumption of *stationarity* states that the mean and variance of a particular variable will not change with the location of measurements. This assumption—technically referred to as first- and second-order stationarity—often catches those new to spatial statistic unawares. Stationarity is likely to be violated when there is an unrecognized gradient in the data (e.g., increasing precipitation or soil nutrient availability), when the underlying sampling methods are of limited extent and fail to measure changes in variables with scale, or when patterns are *anisotropic* (a marked directionality in the data). When non-stationarity exists and is unaccounted for in a statistical analysis, essential statistical parameters (such as mean and variance) will not be universal but location dependent. In landscape data, topographic relief can impose gradients and directionality on spatial data, both of which can violate stationarity assumptions. The usual response to this issue is either to detrend the data (commonly done for time series analysis via linear regression) or to account specifically for these gradients in the statistical model. Spatial analysis programs often assist with this adjustment when correcting for simple, linear trends. However, the removal of nonlinear trends remains difficult and is a continued area of investigation (Fortin and Dale 2005). Some spatial analysis programs provide the option for either isotropic (all-directional) or anisotropic (directional) analyses; the latter allows the user to evaluate spatial dependence and compare model parameters across a range of compass directions.

#6. Interpreting Spatial Statistics Is Both a Science and an Art

As with other kinds of statistical methods, many analysis decisions are up to the user and can be perplexing. For example, some methods (including semivariograms, which are discussed in detail below) involve fitting a theoretical curve to the empirical data and then estimating parameters from this curve to describe the spatial structure in the data. There are a number of different standard curves that may be fit to the data (e.g., spherical, exponential, sinusoidal, linear models), but each may provide strikingly different parameter estimates for characterizing the spatial structure. Selecting the most appropriate model can be done in several ways, but the user ultimately must choose and justify her/his choice. If a study entails estimates of spatial dependence for multiple variables or among multiple landscapes, different variables or plots may achieve their best fit with different models. The analyst must then decide whether to use the best model each time, knowing that the models will vary; or to use the same model for consistency, knowing that the fit will vary. Either way, the quantitative estimates derived from the analysis can be considerably different.

Another issue of interpretation is that empirical data can be very noisy and, thus, not conform nicely to the theoretical curves. How to interpret apparent cycles in the data, or points that fall outside broad confidence intervals, can be challenging. The results of spatial statistical analyses with real landscape data are often much more ambiguous than results of an ANOVA that are based on *F*-ratios with set probability limits. If you encounter such situations, you are not alone. Do not be deterred, but do seek statistical advice from someone experienced with the application and interpretation of these analyses. Because these methods have and will continue to advance, these tasks will soon become more convenient, efficient, and reliable. However, there is no single prescription or cookbook approach—rather each new problem may require novel methods with their associated sets of assumptions and restrictions. Therefore, the user must take care when applying statistical techniques and drawing conclusions from results and remember that the question or objective of the analysis must be unambiguously specified ahead of time.

POINT PATTERN ANALYSIS

The data for point pattern analysis methods are composed of records of event-based spatial phenomena, such as the location of individuals of an invasive species (Schreiber and Lloyd-Smith 2009); the presence of kangaroo rat nest mounds (Schooley and Wiens 2001); or occurrence of lightning caused fire ignitions (Podur et al. 2003). Point data are irregularly distributed in space and characterized by x, y coordinates (the points) with variable supplemental information (the marks) to identify the type of event and relevant biological or physical attributes associated with that point (e.g., species, age, size, soil type, etc.). Once acquired, these spatial point pattern data allow hypotheses linking spatial pattern (the points) to ecological process (the marks) to be examined. Special techniques have been developed to describe these data and to test their association with relevant biological and physical attributes of the landscape (Perry et al. 2006).

Point pattern analysis has a long history of study in ecology. Clark and Evans (1954) first suggested that the mean distance to a nearest neighbor divided by the mean distance of randomly distributed points provided a normalized measure of the departure of spatial patterns from those expected by simple random processes. These calculations, when done by hand in the '50s, were computationally difficult, especially when data sets were large. A different approach was suggested by Greg-Smith (1952) who aggregated point data into quadrats and then used the differences in frequencies between adjacent quadrats as a measure of spatial pattern. Successive increases in quadrat size allowed scale-dependent changes in variance to be estimated (O'Neill et al. 1991; Levin 1992) (see Fig. 5.3). More efficient sampling methods have since been developed to provide more robust estimates (e.g., lacunarity analysis; Plotnick et al. 1993, 1996), but the basic concept of change in variance with scale as a measure of pattern-scale dependency remains useful.

The Clark and Evans (1954) nearest-neighbor calculation produced a single value for each dataset. Ripley (1977, 1979) introduced the *K* function, which examines nearest-neighbor associations over all distances within the dataset, providing a scale-dependent measure for point patterns without the need to aggregate data into quadrats. The *K* function, as described by Crawley (2007), is calculated as:

$$K(d) = \frac{1}{N^2} A \sum_{j} \sum_{i \neq j} \frac{I_{(d)} \langle d_{ij} \rangle}{w_{ij}},$$

where N is the number of points; A is the size of the study area that contains the points; d_{ij} are the subset of distances that are less than $I_{(d)}$ (values of $I_{(d)}$ will range successively from the minimum to maximum possible distance within A); and w_{ij} is an edge correction required to avoid truncation effects when a given point is near the boundary ($w_{ij} = 1$ when a circle of radius I_d around point ij does not contact the boundary of A, and <1 when boundaries are encountered).

All these calculations can be easily done within the *spatstat* library (Baddeley and Turner 2005) of R (R Development Core Team 2010). Baddeley and Turner (2005) provide an example of analysis with Ripley's *K* for a point pattern dataset of Swedish pine trees (Strand 1972; Ripley 1988). The nearest-neighbor analysis reproduced here (Fig. 5.4) shows two lines. The solid line is the expected value at each distance class, $I_{(d)}$, if all points were randomly distributed; the segmented line shows significant deviation of a range of $I_{(d)}$ from ~6 to ~12 (see Baddeley and Turner 2005 for the statistical methods used to test for significant departures from random), indicating that trees were more uniformly distributed than the "expected" (hypothetical) random pattern. The causes of spatial regularity over small distances may include processes such processes as nonrandom seed recruitment or mortality, competition or a nonrandom substrate. The results shown in Fig. 5.4 define the

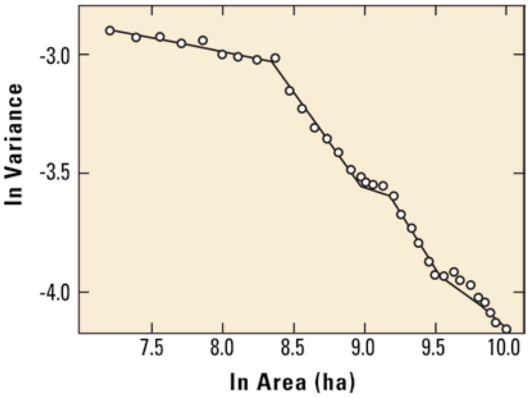


FIGURE 5.3.
Variance in percent grassland in a landscape near Goodland, Kansas changes over a range scales. These changes created a stair-step pattern hypothesized to result from human activities that vary from fields to farms, townships, and counties.

ADAPTED FROM O'NEILL ET AL. (1991).

scales over which future studies may concentrate to identify the specific processes that have resulted in these nonrandom patterns. Of course hypothesis testing requires the uncertainty around these numbers to be estimated. The *spastat* library provides an example of how to estimate uncertainties using Monte Carlo methods.

Perry et al. (2006) and Diggle (2003) provide excellent discussions of other methods for analyzing spatial point patterns. No matter the choice of method, one should be aware that when the study area, A, is very large multiple (new) ecosystems or cover types may be encountered. If points are restricted to a single ecosystem or cover type, then patterns will always appear to be spatially heterogeneous with areas of aggregation within preferred habitats separated by areas of overdispersion; conversely, if spatial extents are very small, then edge effects will be large and results biased despite use of edge correction methods that adjust spatial weights, w_{ij}. As always, there is an intimate dependency between the nature of a dataset, the scale of analysis, and the adequacy of the statistical methods used for description and hypothesis testing.

AUTOCORRELATION AND VARIOGRAPHY

The heart of spatial statistics is the concept of correlation of spatially distributed variables. Autocorrelation and variography are two widely used methods for characterizing spatial dependence, or spatial structure, in a variable as a function of its position in a landscape. These methods are considered *global spatial statistics* because they estimate the intensity of spatial dependence for the entire study area (Fortin and Dale 2005). Both methods also provide estimates of the spatial scale(s) over which data are dependent. Factors that cause spatial dependence may be intrinsic to the system being studied, such as dispersal and competition in biotic

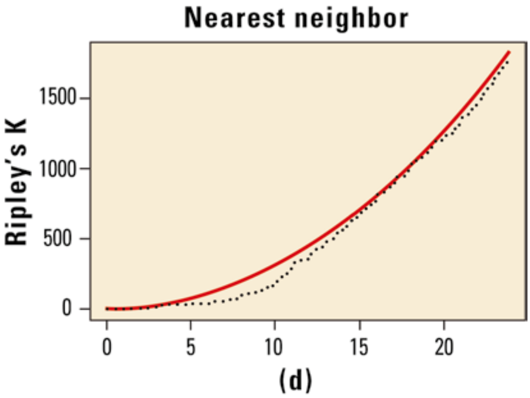


FIGURE 5.4.
Nearest neighbor analysis of the Swedish pine data using Ripley's K and the *spatstat* library of Baddeley and Turner (2005). See text for details of analysis.

communities, and often manifested as fine-scale patchiness. This is certainly the case for measures of species abundances, which are always positively autocorrelated (Lichstein et al. 2002). Factors external to the system, such as topographic gradients of moisture, nutrients, and light, may also induce correlations (as noted above) but these are usually responsible for broad-scale trends (Legendre 1993; Lichstein et al. 2002). Conceptually, any observed spatial structure is a mix of induced spatial dependence (i.e., how the variable is responding to the spatial structure of an exogenous process) and inherent spatial autocorrelation (i.e., intrinsic to the variable or process of interest), but estimates of spatial autocorrelation coefficients cannot discriminate between these different components (Fortin and Dale 2005).

Autocorrelation

Spatial autocorrelation is estimated by taking the average squared difference between all points separated by a given distance, *h*, the "lagged" distance between points. If we assume second-order stationarity (constant mean and variance over the entire dataset), then the autocorrelation for each distance between points, $r_{(h)}$, may be calculated as a Pearson correlation coefficient:

$$r_{(h)} = \frac{\sum_{i=1}^{N-h} (z_i - \bar{z})(z_{i+h} - \bar{z})}{\sigma^2},$$

where z_i is the value at location *i*; z_{i+h} is the value of a point at a distance of *h* from *i*; σ^2 is the overall variance; and *N* is total number of points. A graph of $r_{(h)}$ vs. *h* is a *correlogram* that provides a visualization of the change in the dependency between points as a function of the distance between them, *h*. In general, to assure numerical adequacy of estimates of $r_{(h)}$, *h* should never be calculated for distances greater than ½ the total distance that was sampled, and there should be at least 50 pairs of points for each lag distance (Rossi et al. 1992). Indications of ecological scale can be verified by statistically testing the peak values of the correlogram (both positive and negative) for significant differences from zero (Carlile et al. 1989). The conditions for valid tests for the significance of these peaks are restrictive, requiring (1) that only points separated by *h* are compared for each lagged distance, (2) that gradients of change or trends in the data be removed before correlations are estimated (see Legendre 1993 for other restrictions in the analysis of gradients and autocorrelated data) and (3) that the residuals be normally distributed (Legendre and Legendre 1998).

Because $r_{(h)}$ is normalized by its variance, values will always lie between –1.0 and 1.0, which can be advantageous when comparing correlograms for different variables and/or landscapes. When $r_{(h)}$ is near 1.0, the lagged values are positively related; when $r_{(h)}$ is near –1.0, the lagged values are negatively related; and when $r_{(h)}$

is close to 0.0, the values are spatially independent. Of course, statistical tests are used to show when values of $r_{(h)}$ do not differ from 0.0 and to determine the minimal separation distance, h_c, beyond which the data can be considered spatially independent.

Let's consider an empirical example. In an area that was severely burned by the 1988 Yellowstone Fires, the density of postfire lodgepole pine (*Pinus contorta* var. *latifolia*) seedlings was recorded sequentially in 1-m^2 plots ($N = 3395$) at every meter along a 3.4-km transect that spanned a large patch of burned forest. The raw count data (seedlings m^{-2}, depicted in Fig. 5.5a) clearly show variability along the transect. To quantify spatial structure of the postfire tree seedlings, autocorrelation of lodgepole pine seedling density was calculated for all pair plots separated by lag distances, h, ranging from 1 to 250 m to generate a correlogram (Fig. 5.5b). The analysis revealed very strong spatial autocorrelation over short distances and a

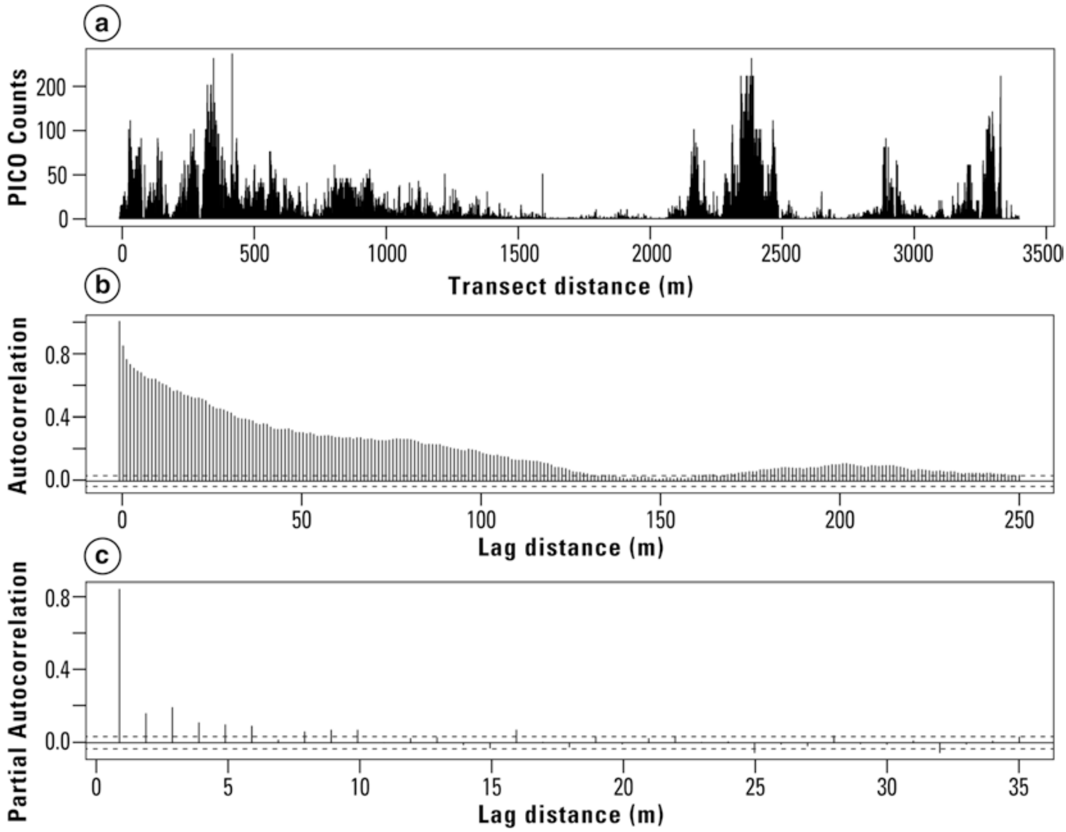


FIGURE 5.5.

(**a**) Continous counts of postfire lodgepole pine seedlings in 1-m^2 plots at 1-m intervals along a 3.4-km transect in Yellowstone National Park in 1991, 3 years after the 1988 fires (Turner et al. 1997b). (**b**) Autocorrelations and (**c**) partial autocorrelations of the lodgepole pine seedling counts steady decline as lag distances increased. Correlation diminished with distance, declining to $r = 0.40$ at a lag distance of about 40 m, and to $r = 0.20$ at about 90 m. Because the sample size was so large, even very small correlations were statistically significant at $p = 0.05$, indicated by the blue dashed line in Fig. 5.5b. Thus, this example also demonstrates another important point: when sample size is very large, statistical significance doesn't always reflect ecological importance. Under such circumstances, one may set the limit of spatial correlation to a meaningful value; for instance, if $r_{(h)} = 0.2$ at a given distance h, then only ~4 % of the variance is accounted for by spatially correlated processes at that distance. Applying this to our example, we could infer minimal spatial autocorrelation between samples separated by at least 90 m.

Measures other than the Pearson correlation coefficient, such as Moran's I and Geary's c, can also be used to test for spatial dependence (Fortin and Dale 2005). Interpretation of Moran's I is very similar to interpretation of a correlation coefficient (Fig. 5.6). The magnitude of Moran's I, as well as the sign, are both important. The magnitude of the absolute value of Moran's I (on the y axis) in the correlogram of the random landscape (Fig. 5.6a) is about 0.12, indicating little spatial autocorrelation at any lag distance; in contrast, the maximum absolute value of Moran's I in a landscape with a gradient (Fig. 5.6b) approaches 1.0, indicating very high spatial autocorrelation over some lag distances. In a landscape with repeated patterns (Fig. 5.6c), the strength of the autocorrelation is intermediate. The sign of Moran's I is again informative. As with a traditional correlation analysis, a positive value indicates positive correlation, and a negative value indicates a negative correlation. When there is a repeated pattern, correlations will be positive at short distances, then become negative (peaks to valleys), then become positive again (peaks to peaks; Fig. 5.6c). Autocorrelation methods are useful for defining spatial dependencies and for discriminating between positive and negative autocorrelations, but they are unable to distinguish between certain kinds of spatial patterns, such as sharp step change vs. a gradient (Palmer and McGlinn 2016).

Pearson correlation coefficients may be used not only for their simplicity, but also because measures of the direct effect at each distance h can be estimated by the partial autocorrelation coefficient (Fig. 5.5c). The partial correlation coefficient is the autocorrelation between points separated by h that has first been adjusted for correlations at all other distances and therefore represents the unique effect of points z_i on z_{i+h}. Figure 5.5c shows that the range of distances with significant direct effects (as measured by the partial correlation) is small (~10 m) in the lodgepole pine transect data, although accumulated indirect effects (as measured by the simple correlation, Fig. 5.5b) extend to ~130 m. Thus, abundance levels correlated over relatively short distances (the partial correlation) nevertheless result in patches of high abundance at scales of ~130 m (Fig. 5.5b).

When data for a spatial autocorrelation analysis come from a linear transect, directionality is not a concern. However, if the data come from a two-dimensional

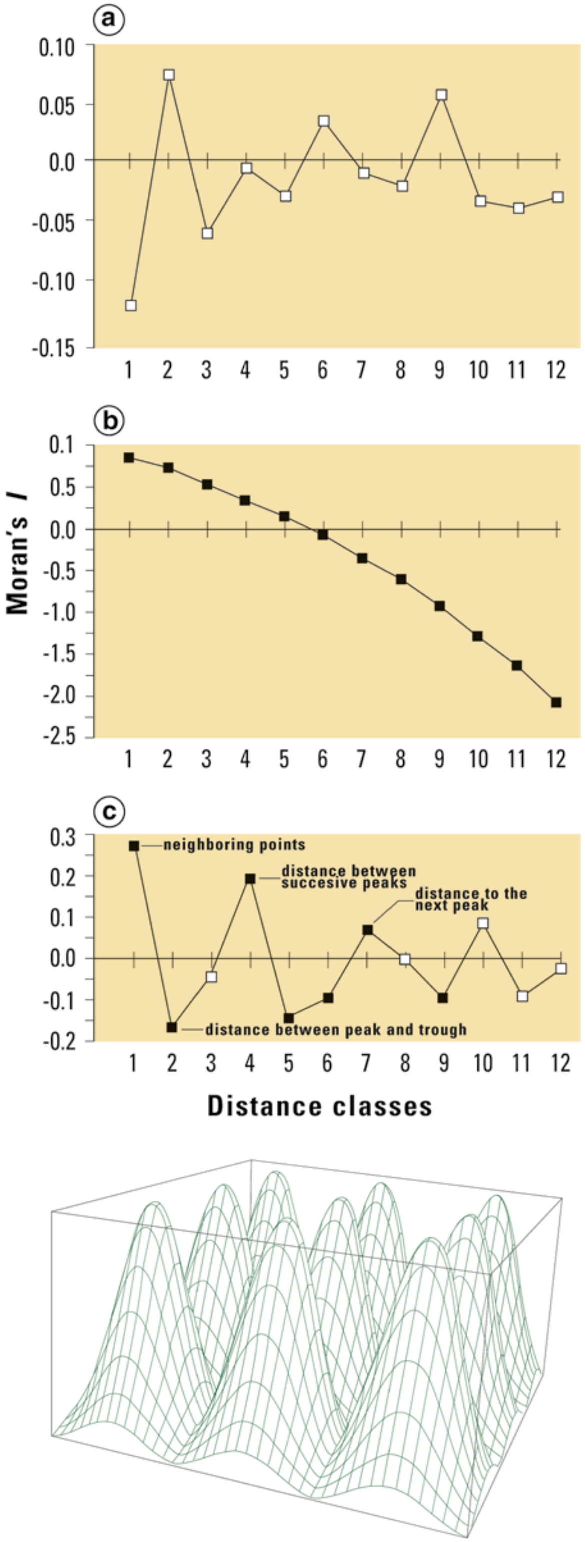


Figure 5.6.

All-directional spatial correlograms of artificial landscapes: (**a**) random landscape, (**b**) landscape with a gradient, and (**c**) landscape with a repeating pattern, the “nine fat bumps” shown below. Note that Moran’s I behaves like a correlation coefficient.

Adapted from Legendre and Fortin (1989).

area, directionality should be considered. For most analyses, the default is to derive the coefficients from an omni-directional (isotropic) analysis, meaning that all pairs of points at a given lag distance are used, regardless of the directionality between them. However, it is possible that the intensity of spatial dependence differs by direction, and analyses may be computed for pairs of points that lie in the same direction (anisotropy). For example, autocorrelation could be measured in both an east-west and a north-south direction and the two sets of coefficients compared.

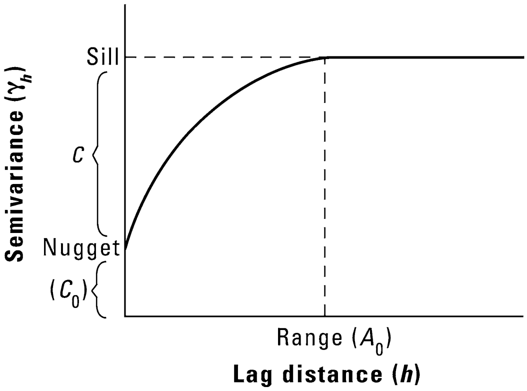
Variography

Variography is also based on spatial dependence among pairs of observations at different lag distances, but it uses a direct measure of variance in the computation and allows for spatial interpolation of point data across a landscape. Kriging techniques have been developed for this purpose with the *semivariance*, $\gamma_{(h)}$, providing the needed estimate of spatially dependent variance. The semivariance is equal to half of the squared difference of all pairs of points separated by distance h (Rossi et al. 1992; Palmer 1992) and is calculated for each lag distance, h as:

$$\gamma_{(h)} = \frac{N_{(h)}}{2} \sum_{i=1}^{N_{(h)}-l} \left(z_i - z_{i+h}\right)^2 ,$$

where z_i is the value at location i; z_{i+h} is the value of a point at a lagged distance of h from i; and $N_{(h)}$ is number of pairs examined at lag distance h. Plotting $\gamma_{(h)}$ over all values of h results in a *variogram*, the central tool of geostatistics (Rossi et al. 1992). In an idealized variogram (Fig. 5.7), semivariance is minimal when h is small, then increases steadily until a distance is achieved where further increases in h no longer cause the variance to increase. As with autocorrelation analysis, variography depends on several underlying assumptions, including absence of a trend in the z values across space, that variance is constant across the dataset, that the precise location of each observation does not matter (only the distance between

FIGURE 5.7.
Idealized semivariogram showing the nugget (C_0), sill ($C_0 + C$), and range (A_0); see text for explanation.



points is important), and (for an isotropic variogram) that the magnitude of h matters, but not the direction.

Interpretation of spatial dependence using variograms is based on several key parameters. The asymptotic value of $\gamma_{(h)}$ as h becomes very large is called the *sill*. The distance over which variance increases until the sill is reached is called the *range* (A_0, Fig. 5.7). The range is one of the most important parameters extracted from a variogram because it defines the distance (or scale) of spatial dependence in the data; at distances greater than the range, the data are considered to be spatially independent. Finally, there is often some amount of variance that is not related to spatial structure in the data, at least over the scales that were examined. This variance is estimated by the y intercept of the variogram and is called the *nugget*, typically denoted as C_0 (Fig. 5.7). The nugget includes variance at scales smaller than the minimum separation distance between points and variance attributed to changes through time as data were sampled, measurement error, and random sampling error. The structural variance, C, is the difference between the sill and the nugget. The overall magnitude of spatial dependence in the data can be estimated by computing the proportion of structural variance, calculated as structural variance divided by the sill, or $[C/(C_0+C)]$. When there is no nugget or C_0 is small relative to C, the proportion of structural variance is high, and there is considerable spatial dependence in the data. When C_0 is nearly equal to the sill, there is no spatial dependence in the data. When the semivariance continues to increase with lag distance, h, and does not level off, it means that there is spatial dependence over all measurement scales. In this case, estimates of the range, A_0, will exceed the maximum value of h; in other words, the range will be greater than the largest lag distance that was analyzed. Estimates of semivariance are unreliable when there are too few pairs of points for any given lag distance, which is often the case as h becomes large. Thus, the sampling restrictions for variogram estimation are the same as those given above for autocorrelation. Variograms should be calculated only for lag distances up to half the actual distance over which the data are measured, and it is best to include at least 50 pairs of points when calculating semivariance for each lag distance.

To estimate the nugget, sill, range, and proportion of structural variance from a variogram, a theoretical model must be fit to the plot of $\gamma_{(h)}$ vs. h (Fig. 5.8). Spherical, exponential, and linear models are commonly used theoretical models, and analysis programs will report C, C_0, and A_0 values. Different models may produce different numerical estimates for these parameters, and the best choice for a theoretical model may be difficult to determine a priori. Most practitioners will inspect the shape of the empirical variogram, then fit several models to determine which one provides the best fit by comparing the proportion of structural variance among models and examining r^2 or AIC values. This can be straightforward when a single variogram is being evaluated. However, when a study involves multiple variograms, different theoretical models may fit best for different response variables or plots (Fig. 5.8). The analyst must then decide whether to use one theoretical model

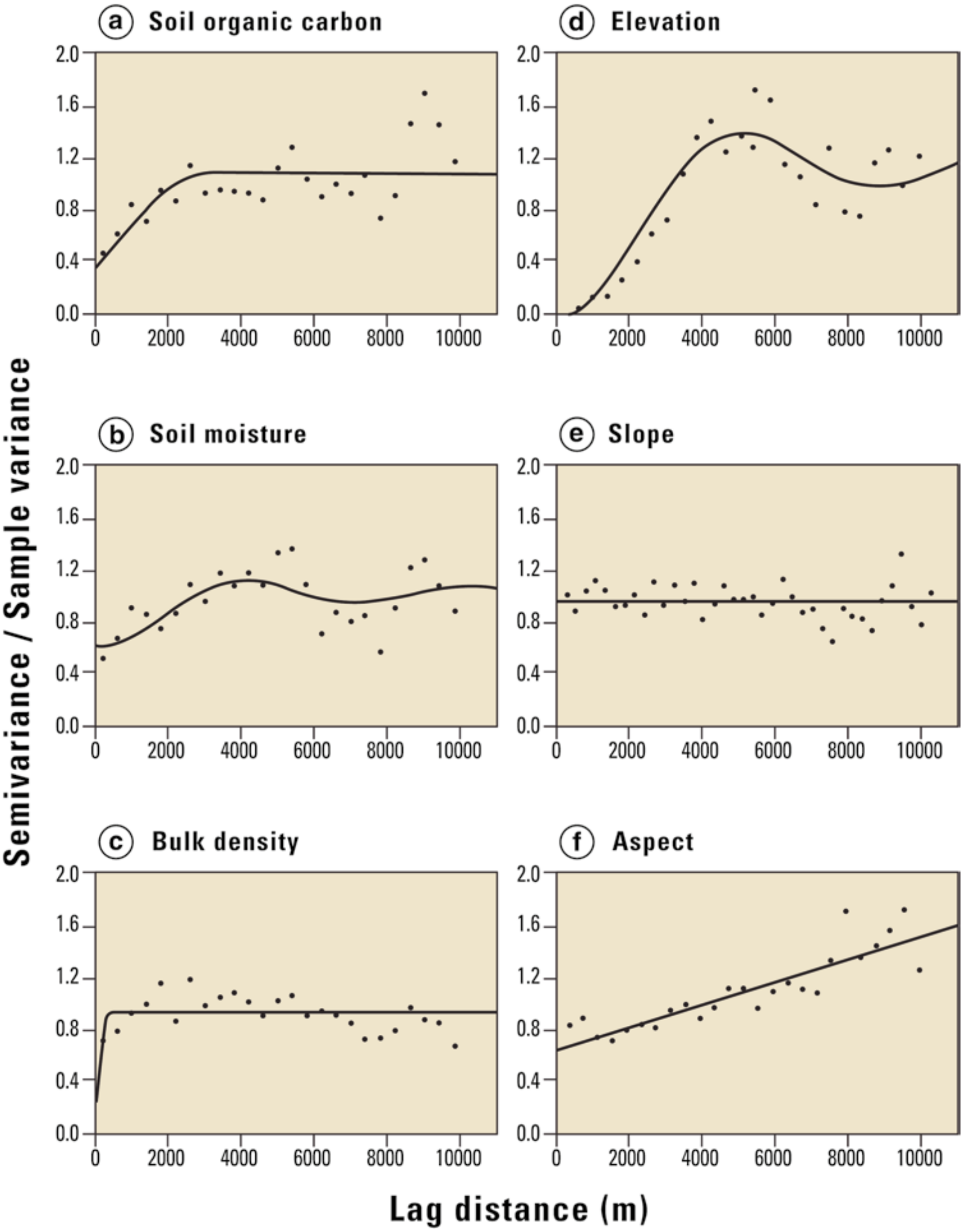


FIGURE 5.8.

Illustration of six models for fitted semivariograms using data from the Luquillo Experimental Forest of Puerto Rico: (a) soil organic carbon, fit with a spherical model; (b) soil moisture, fit with a wave/hole model; (c) bulk density, fit with a spherical model; (d) elevation, fit with a wave/hole model; (e) slope angle, fit with a random model; and (f) aspect, fit with a linear model. The equations for the illustrated semivariance models are: Random γ = mean sample variance; Linear $\gamma(h) = C_0 + C[(h/A_0)]$; Spherical $\gamma(h) = C_0 + C(1.5(h/A_0) - 0.5(h/A_0)^3]$, $h \leq A_0$; $\gamma(h) = C_0 + C$, $h \geq A_0$. Wave/hole $\gamma(h) = C_0 + C\{1 - [\sin(A_0 * h) * h/A_0]\}$.

ADAPTED FROM WANG ET AL. (2002).

(e.g., the spherical model) for all data, thereby minimizing the effect of changing the model on parameter estimates, or to use the best model fit for each dataset. In our experience, different models for different processes are appropriate, but statisticians will differ in their opinions, and thinking about this topic may change—points the analyst should keep in mind.

The idealized curve for a variogram with a distinct scale of spatial autocorrelation is asymptotic, but empirical variograms may take a surprising number of shapes (Fig. 5.8); real-world data can be messy! If a spatial dataset is nonrandom and has been adequately sampled (i.e., the spatial extent of the data provides an adequate representation of the pattern of interest) then we expect the variogram to ascend from an initial value at $h = 0$ to an asymptotic value (Fig. 5.8a, d). Variograms that do not asymptote, but rather continue to increase as h increases (Fig. 5.8e), indicate an underlying trend or nonstationary stochastic process (Crawley 2007) which must be accounted for before finer scale dependencies can be explored. A relatively flat horizontal variogram indicates a pattern that lacks spatial dependencies (i.e., a random pattern, Fig. 5.8c).

The form of the variogram does not lend itself to statistical testing, but confidence intervals for semivariance estimates can be calculated (Shafer and Varljen 1990; Zheng and Silliman 2000; Lin and Chen 2005; Xiao et al. 2005). Because the estimate of semivariance for each lag distance is obtained from multiple pairs of points, the variance around each estimate can be determined. It is increasingly common for a 95 % confidence interval to be plotted in empirical variograms. Although confidence intervals will often bounce around the sill, they are helpful in determining the range over which significant changes in variance may be expected (Xiao et al. 2005). Significance testing for each lag distance h is not commonly done in variography (in contrast to correlograms), but the occurrence of a semivariance estimates below the 95 % confidence interval usually corresponds to a significant autocorrelation at that lag distance.

Spatial interpolation, or kriging (Rossi et al. 1992), uses the semivariogram to predict an expected value at unmeasured locations. Kriging methods predict z by using a weighted average of the expected values based on the distance from other points, with the weights accounting for autocorrelation in the observed data. Results yield a best linear unbiased estimate of a variable at a given point. Kriging has found many ecological adaptations, including mapping vegetation community distributions (Arieira et al. 2011), determining patterns of exotic species invasion (Cilliers et al. 2008; Schreiber and Lloyd-Smith 2009) and locations of exotic weeds (Kalivas et al. 2012), and designing optimal spatial sampling methods (Xiao et al. 2005).

Although semivariance has many similarities to the autocorrelation function (Box 5.1, and see Fig. 1 in Palmer and McGlinn 2016 for helpful comparisons), there are several notable differences between these methods that affect their use and interpretation. Because correlograms emphasize the strength of the correlation

BOX 5.1

GENERAL RELATIONSHIPS BETWEEN THE AUTOCORRELATION AND SEMIVARIANCE OF VALUES LAGGED BY DISTANCE *H* (ADAPTED FROM ROSSI ET AL. 1992)

If the population mean and variance are constant (i.e., there is no trend) and $C(h) = \text{thecovariance} = 1/N(h)\sum(z_{-h} - \bar{z}_{-h})(z_{+h} - \bar{z}_{+h})$, where $-h$ and $+h$ represent the head and tail of data points separated by distance *h*, then:

$$\gamma(h) = \sigma^2 - C(h)$$

$$\rho(h) = C(h)/\sigma^2$$

$$1 - \rho(h) = \gamma(h)/\sigma^2$$

where $\gamma(h)$, $\rho(h)$ are the semivariance and autocorrelation, respectively, for points separated by distance *h*.

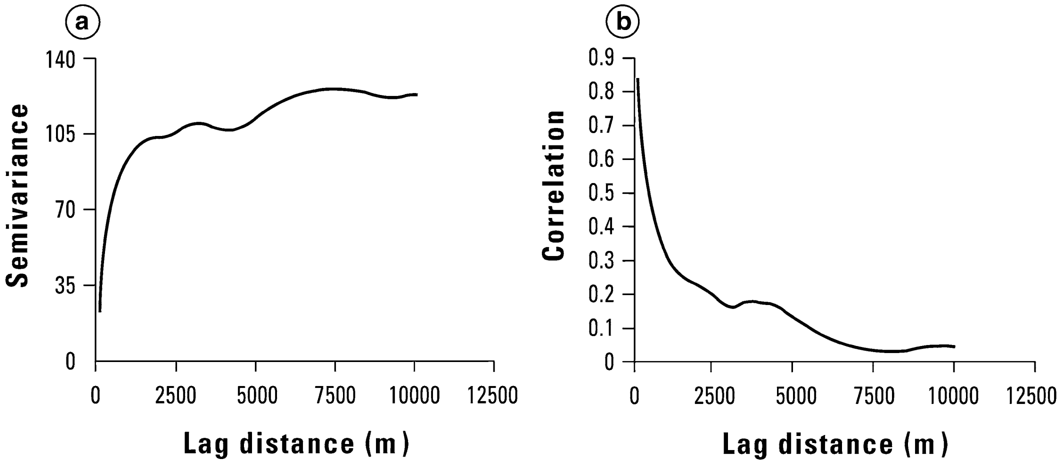


FIGURE 5.9.
Example semivariogram (**a**) and correlogram (**b**) computed for a landscape in northern Yellowstone National Park. Note that the shape of the correlogram is nearly identical, although inverted, to the shape of the semivariogram of the same data. These two approaches are complementary.

ADAPTED FROM MEISEL AND TURNER (1998).

at each lag distance and variograms report the magnitude of the variation (Box 5.1), the empirical plots are of opposite shape (Fig. 5.9). The semivariance estimates, which are not normalized by either the mean or the variance, may take on any positive value as all forms of variance also do. However, the magnitude of the semivariance is informative when comparing variables measured in the same units—for example, one could ask whether the total amount variance in plant biomass is increasing across a chronosequence of plots, or is greater in certain landscapes than in others. When comparing variograms for variables that are reported in different units (e.g., plant biomass in g and soil nutrient properties in ppm), the magnitude of variance cannot be readily compared. In such cases, variograms may be standardized by dividing by the maximum semivariance ($C + C_0$) so that the y axis scales from zero to one. This normalization allows the shape of the curve and the range estimates (A_0) to be easily read and interpreted, regardless of the units in which semivariance was reported. In contrast to correlograms, semivariograms provide no information about whether spatial dependencies are positive or negative because variances are always positive. Lastly, one might expect that *range* estimates would be the same for correlograms and variograms. This is not always the case because the semivariance measures an asymptote where variance no longer increases with distance, whereas autocorrelation measures multiple distances where autocorrelation is present rather than extracting a single dominant scale.

Cross-Correlograms and Co-variograms

When multiple variables are recorded in either space or time then the correlations among these variables can be used to more accurately describe and predict the spatial patterns of one or more predicted variables (Kalkhan and Stohlgren 2000; Kalkhan et al. 2007). The additional information provided by these cross-correlations allows a reduction in the total number of samples needed to detect significant effects (Fortin and Dale 2005). Covariance analysis has long been an essential element of regression methods (Cressie 1991) and may also be used to advantage with kriging (referred to as *co-kriging* when cross-correlations are used) to improve estimates of spatial interpolations. Although co-kriging is a more complicated process and long-regarded as a difficult computation (Deutsch and Journel 1998), advanced methods are now available making the use of spatial cross-correlations among multiple predictor variables an attractive option (see gstat package in R Development Core Team 2010; Rossiter 2012). For instance, precise knowledge of the spatial distribution of perennial weeds, which flourish in cotton agriculture, would allow better-targeted management options to be developed and employed. If the distribution of weeds could be estimated as a function of environmental variables, measured at lower expense, then significant savings would be realized by the use of co-kriging methods (Rossiter 2012). Kalivas et al. (2012) used this approach to reduce prediction errors over ordinary kriging (Fig. 5.10) with co-kriging providing better estimates of the distribution of bindweed and purple nutsedge, two difficult weeds to control (Kalivas et al. 2012).

More advanced statistical methods hold great promise for landscape studies but, unfortunately, are beyond the scope of this chapter. The reader may wish to refer

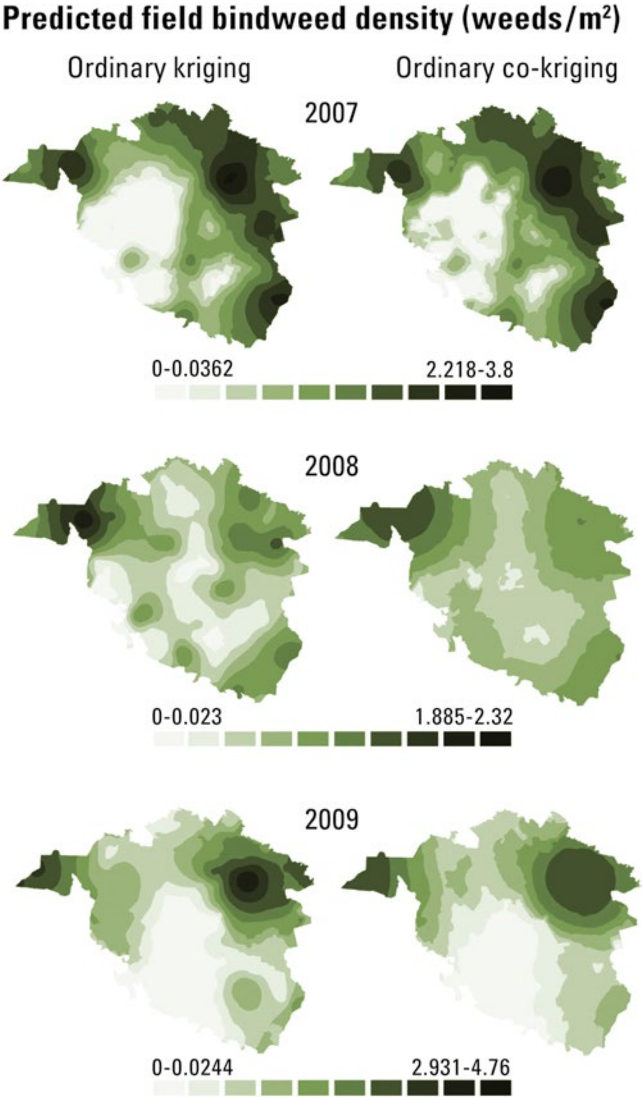


Figure 5.10. Interpolated maps of field bindweed density with the use of ordinary kriging (**a**) and co-kriging (**b**) for three different years (Reproduced with permission from Kalivas et al. 2012).

to appropriate texts (e.g., Cressie 1991; Fortin and Dale 2005; Ripley 2005) and articles (e.g., Wagner and Fortin 2005; Perry et al. 2006), which provide guidance and caveats for use of additional multivariate methods to describe and predict spatial patterns.

Optimized Sampling Designs for Spatial Statistics

When landscape ecologists think about evaluating spatial dependence using a field study, the default plan is often to sample continuously along transect (as was done for the lodgepole pine seedlings in Fig. 5.5) or within a full uniform grid of points. However, these are inefficient, not only because they take a lot of work, but also

Table 5.1.
Examples of cyclic sampling designs (adapted from Burrows et al. 2002), where x is the length of the cycle and sample locations are given in the same units (e.g., meters).

Cycle definition	Length of cycle (x)	Number of plots sampled per cycle	Sample locations (0 to $x-1$)	Illustration of sampling cycle (+indicates sample location, o is not sampled)
2/3	3	2	0, 1	+ + o
3/7	7	3	0, 1, 3	+ + o + o o o
4/13	13	4	0, 1, 3, 9	+ + o+o o o o +
5/21	21	5	0, 1, 4, 14, 16	+ + o o+o o o o o o o o o+o+o o o o

A 3/7 cycle indicates that three plots in every seven are measured. When repeated, the spacing of the three plots will give pairs of plots separated by one, two, three, four, five, six, and seven lag distances

because they produce data in which the point pairs for short lag distances are overrepresented, and the point pairs for long lag distances are underrepresented. Sampling designs that systematically vary the distances between sample points then repeat that sequence can produce a dataset with similar numbers of point pairs across all lag distances (Table 5.1). These clever designs will give comparable statistical power over a range of lag distances and are thus a valuable alternative to systematic sampling schemes. Because the repeated distances are considered to be a cycle, these sampling designs are often referred to as *cyclic*. As an example, consider sampling a 1000-m transect at 1-m intervals with traditional protocols that would produce 1000 data points. If 4/13 cyclic sampling was used instead in place of complete sampling (Table 5.1), then approximately 300 sampling points could efficiently measure a wide range of lag distances. There is detailed treatment of these methods in Cressie (1991), but we also recommend Burrows et al. (2002) for an accessible explanation and discussion. Burrows et al. (2002) compared different approaches (random, uniform, and cyclic sampling) for quantifying the spatial pattern of leaf area index (LAI) measures in terrestrial ecosystems that surrounded an eddy flux tower. They found a 60 % reduction in effort required for cyclic sampling designs vs. random and uniform sampling. As with all study designs, pilot data can be extremely valuable for figuring out the best cycle of distances to repeat.

In another example, Turner et al. (2011) used a cyclic design to determine how aboveground vegetation and soil nitrogen availability changed within forested plots following stand-replacing fires. Because these measurements are very labor intensive and the laboratory analyses costly, an alternative to sampling a full grid was desired. In each of four plots, they used a cyclic design ($n = 81$ points) with a minimum separation distance of 2 m between sampling points and a cyclic sequence

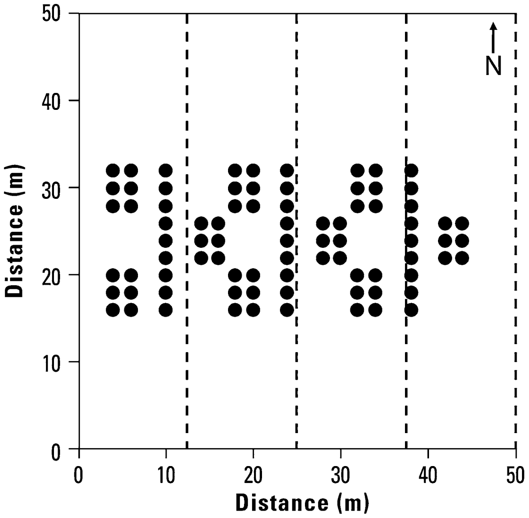


FIGURE 5.11.
Illustration of how a 3/7 cyclic sampling design (see Table 5.1) was implemented to sample soils and aboveground vegetation in Greater Yellowstone (adapted from Turner et al. 2011). The 3/7 scheme is applied in the horizontal direction and reverses direction for the middle three transects.

of points that was repeated (Fig. 5.11). The grid covered an 18 m × 40 m area positioned in the center of each 0.25-ha plot and included nine parallel rows, each separated by 2 m. The 2-m spatial resolution was based on the observed patchiness of aboveground vegetation given our focus on the relationship between vegetation and soil nutrients. Each row included three 3/7 cycles that were 14 m long in which 3 of 7 grid points (the 0, 1, 3 design in Table 5.1, which translated to samples at 0, 2 and 6 m in each cycle) were sampled; the middle three rows were offset by 6 m to account for potential anisotropy. Variography was then used to assess spatial dependence in vegetation and soil variables over 4 years. Using spatial statistics to improve sampling design is extremely valuable in any studies that include the goal of detecting the magnitude and scale of spatial variation in the data.

EXAMPLES OF SPATIAL STATISTICS IN LANDSCAPE ECOLOGY

Because spatial statistics are less familiar than landscape metrics for many landscape ecologists, and therefore not used as frequently, we conclude this chapter with a few additional examples to illustrate the diversity of applications in landscape ecology. As is the case throughout this book, the selected examples are not intended to exhaustive but rather to illustrate how these methods can be used to gain insights into landscape-level questions. We also suggest software resources that readers may find useful (Box 5.2).

Spatial statistics have been used in several studies assessing organism responses to spatial variation in their habitat. The persistence of elephant populations in

BOX 5.2
THE PRACTICAL SIDE: SELECTED SOFTWARE FOR SPATIAL STATISTICS

There are many options for computing spatial statistics, including utilities within widely used GIS software programs such as ArcGIS. We highlight a few here. There are many online resources that provide current developments in spatial ecology including Wikipedia http://en.wikipedia.org/wiki/Spatial_ecology with lists and links to open-source GIS software (http://en.wikipedia.org/wiki/Category:Free_GIS_software). For hands-on learning, we recommend two chapters in the second edition of LEARNING LANDSCAPE ECOLOGY. Exercises developed by Palmer and McGlinn (2015) lead students through the calculation and interpretation of correlograms and semivariograms using Excel and R; this is a great starting point. Exercises developed by Turner and Simard (2016) are more advanced, use GS+ (see below), and are designed to compare and contrast insights gained from traditional landscape metrics and spatial statistics.

R Software. There are a wide variety of utilities available for reading, writing, display, and analysis of spatial data in R. The R software and associated libraries may be explored and downloaded at http://www.r-project.org/foundation/. An overview of the many resources within R may be found at http://cran.r-project.org/web/views/Spatial.html. Libraries used in this chapter include *spatial* and *spastat* for point pattern analysis and *gstat* for geostatistics.

GS+ is commercially available software published by Gamma Design Software, LLC; see http://www.gammadesign.com/. GS+ is a comprehensive geostatistics program that is menu driven and easy to use, and it readily produces kriged maps from empirical variograms. Users should take care to specify the minimum separation distance, however, as this program defaults to bins that may be larger than desired. Demo versions of GS+ can be downloaded for free and used for a limited time.

PASSaGE, which is an acronym for Pattern Analysis, Spatial Statistics, and Geographic Exegesis, is a free and integrated software package for spatial analysis and statistics (Rosenberg and Anderson 2011). It incorporates a wide range of analyses, including point pattern analyses, correlograms, semivariograms, and many more. The developers work in computational biology, bioinformatics, and landscape genetics. See http://www.passagesoftware.net/index.php

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Zimbabwe is being threatened by continued conversion of natural habitat into agricultural lands. Murwira and Skidmore (2005) wanted to determine whether and how the spatial distribution of the African elephant (*Loxodonta africana*) responded to the spatial heterogeneity of vegetation cover based on data obtained in the early 1980s and 1990s. The distribution of elephants was measured from direct counts, and vegetation cover was derived from remotely sensed data. Variography applied to these data produced measures of the dominant scale (i.e., the range) and intensity (the sill) of the normalized difference vegetation index (NDVI) in 3.84-km × 3.84-km windows distributed in a 61-km × 61-km landscape. The range and sill were then used as predictor variables of elephant occupancy within mixed-use landscapes and to determine mixtures that optimized probability of elephant occurrence (Fig. 5.12). Examination of trends in agricultural intensity

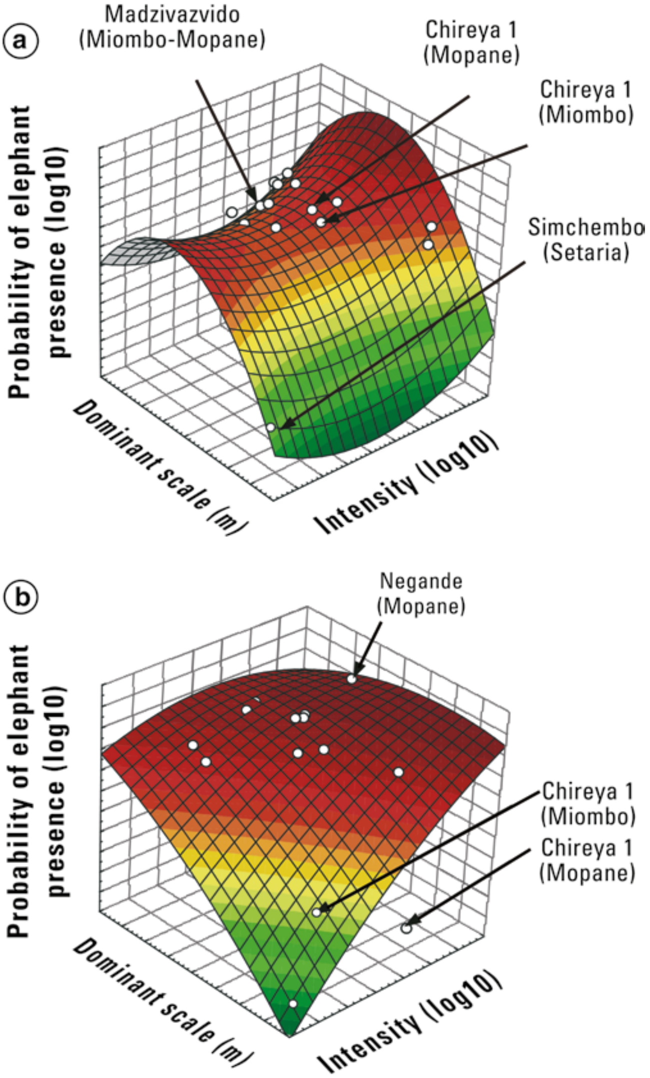

FIGURE 5.12.
The dominant scale and intensity of spatial heterogeneity in vegetation cover jointly influence the probability of elephant presence in (**a**) the 1980s and (**b**) the 1990s in an agricultural landscape in Zimbabwe.

ADAPTED FROM MURWIRA AND SKIDMORE (2005).

were found to be moving vegetation patterns away from an optimum mixture towards uniform agricultural areas which would not allow continued persistence of elephants within these landscapes.

Another example comes from a study of winter habitat use by woodland caribou (*Rangifer tarandus caribou*) in Newfoundland, Canada that blended geostatistical analyses with habitat selection (Mayor et al. 2007). Through careful analyses of multiple levels of habitat use (seasonal range, travel routes, feeding areas, and microsites) in response to snow depth and the abundance of lichens, Mayor et al. (2007) found that caribou reduced the variance in these key habitat features by selecting favorable habitat. By comparing variability of habitat components measured at four levels of habitat use (from feeding microsites to population winter range) across a spectrum of spatial scales (from 1 to 28,000 m), Mayor et al. (2007) showed that caribou first selected for lichens at a broad scale (13 km) then selected areas with shallower snow at all scales.

In a landscape study of plant–animal interactions, De Jager and Pastor (2009) used spatial statistics to evaluate how available and consumed browse has changed with time in Isle Royale National Park, Michigan (USA) as the size of the moose (*Alces alces*) population declined. Four different variogram models were fit to measured levels of moose consumption, browse biomass, plant basal area, and soil fertility; each model representing a different type of landscape pattern from random to regularly arranged patches. The best models were then fit to patterns of browse availability, nitrogen availability, and conifer basal area. The low levels of moose populations have resulted in declining levels of annual consumption which, in turn, have resulted in random distributions of browse consumption: there were simply too few moose to impose detectable spatial patterns as occurred in the past. It appears that lower grazing levels have resulted in new process-pattern relationships with current vegetation patterns more related to variation in fertility, light availability through the canopy and canopy gaps, or seed dispersal patterns than to moose consumption (De Jager and Pastor 2009).

Spatial statistics are also useful in studying ecosystem properties such as nutrient pools and flux rates (e.g., Fig. 5.8, Wang et al. 2002). For example, Vasquez et al. (2012) explored the relationship between total soil carbon and hydrologic and biotic processes in a subtropical landscape in Florida, USA. They studied three nested regions and found that total soil carbon varied at two key scales, one over a relatively short range (5.6 km) in association with local soil and landscape variation, and another at a longer range (119 km) in association with regional variation. Spatial statistics have also detected pattern at multiple scales in a seascape and been used to map seagrass cover. In an estuary in eastern Canada, Barrell and Grant (2013) used acoustic data to detect aquatic vegetation, then used these data to map seagrass beds. Semivariograms were computed, and kriging was used to map seagrass cover and identify "hot spots" where seagrass cover was high relative to the mean.

The above examples employed methods related to variography. Many other examples may be found using autocorrelation (Ishihama et al. 2010; Liang 2012), spectral analysis (Jollineau et al. 2008; Huang et al. 2009), Bayesian statistics (Romero-Calcerrada et al. 2008; Fitzpatrick et al. 2010), and spatial modeling (Kellogg et al. 2008).

As the science of landscape ecology matures, studies will continue to rely on the considerable power of analysis available from methods based on spatial statistics. Because the data and methods of spatial statistics differ from those using landscape metrics, each approach will provide unique and important insights into the broad-scale patterns of ecological processes. The use and interpretation of categorical landscape metrics are understood to a much greater degree than for spatial statistics. The latter seem more difficult for many students to grasp, and the parameter estimates more abstract. Studies that systematically compare results from these two approaches will be most effective in advancing our understanding of landscape dynamics. There is tremendous opportunity for developing richer interpretations of spatial statistics and exploiting the potential for hypothesis testing in landscape ecology. As georeferenced data become more readily available (e.g., through sensor networks and other remotely sensed measurements), there is much to be gained from greater exploration of how to enhance the use of spatial statistics in hypothesis testing.

SUMMARY

Spatial statistics are widely applied in landscape studies for quantifying the spatial structure of spatially distributed data represented by real numbers. The diversity of methods available and the proliferation of jargon used in spatial statistics makes their appropriate use a demanding endeavor. Spatial statistics do not require the a priori categorization of landscape data, nor do they assume a patchy structure with delineated boundaries. Spatial statistics quantify the magnitude of variance in the data, the proportion of that variance that is spatially dependent (i.e., spatially correlated), and the distances over which variables are spatially dependent. These methods differ from, but are complementary to, those based on landscape metrics (Chap. 4).

Landscape ecologists use spatial statistics for wide variety of purposes, but three are particularly important. First, spatial statistics are used to test for independence in spatially distributed data prior to use of parametric statistics for hypothesis testing. When data are spatially dependent (i.e., the degree of correlation between observations changes as a function of distance), statistical tests for hypothesis testing may lead to Type I error (false rejection of the null hypothesis) unless corrective measures are taken. When data are spatially correlated, an adequate separation distance between samples may allow the assumption of spatial independence to be met. Alternatively, methods that adjust and remove spatial dependence prior to statistical testing may be used. Second, spatial statistics are used to quantify the nature of the spatial structure in continuous variables. The magnitude and scale of spatial dependence can be informative and used explicitly to test hypotheses about spatial structure. Third, spatial statistics are used for spatial interpolation, using values at sampled locations to predict values at locations that were not sampled or to produce a continuous surface or map of expected values.

There are several important points to keep in mind when analyzing spatial patterns. Reviewers of grant proposals and manuscripts now expect that the spatial dependence in a dataset has been considered and characterized. Although long considered a nuisance, spatial autocorrelation is not always a problem, but rather an informative attribute of the data leading to new insights and hypotheses. When multiple variables are considered, and similar scales of dependency are found, we now know that this, alone, does not prove causality. However, the coincidence of scales does suggest linkages that are worth exploring. As with all spatial data, the grain and extent of the data strongly affect results of any analysis. Of course, the analyst also must attend to the assumptions required for spatial statistics, including that of stationarity.

One set of methods used in spatial statistics is point pattern analysis, which is used for data formed from event-based records (e.g., location of nest sites). Geographically referenced events have had a long history of study in ecology, and approaches include quadrat-based measures that explore change in variance with scale. Ripley's K function provides a scale-dependent measure that does not require aggregating data into quadrats.

Another set of methods is based on correlation among spatially distributed variables. Autocorrelation and variography measure changes in the relatedness or variance of continuous measurements (such as a rate) as a function of the distance, h, between measured points. Correlograms and variograms provide similar but not identical insights; correlograms indicate the direction and magnitude of autocorrelation, whereas variograms change in variance with distance. Variograms provide the means to interpolate data across space using parameters such as the nugget, sill, and range.

The downside of spatial statistics is that very large datasets may be required to assess the change in pattern across space. However, efficient sampling designs can reduce sampling redundancies (i.e., numerous samples taken at short distances and few samples at long distances) by systematically changing the density of sample points as h increases. An illustration of the efficiencies gained using a cyclic sampling design is presented in this chapter and shows how samples may be arranged to greatly reduce sampling efforts.

As the science of landscape ecology continues to mature, studies will increasingly rely on the considerable power of analysis available from methods based on spatial statistics. Hypothesis testing based on spatial models and spatial statistical tests from replicate study areas is becoming the norm. There is much opportunity and considerable excitement for developing richer interpretations using spatial statistics and exploiting the potential for greater rigor in hypothesis testing in landscape ecology.

DISCUSSION QUESTIONS

1. Gradients due to elevation change often produce spatial correlations in ecological data. How would one design a sampling scheme to separate these correlations from other factors due to biological process of interest (e.g., effects of dispersal patterns on species abundance).
2. Disturbances that change habitat will alter patterns of spatial association for species residing in those habitats. What methods of analysis would you use to characterize the change in scale following disturbance and then monitor the recovery of spatial dynamics with time? What data would be required for your selected method(s)?
3. What will a correlogram of species abundances look like in: (a) continuous, optimal habitat; (b) a landscape with a steep elevation gradient; (c) in a patchy, disturbed landscape?
4. Why does normalization of a statistic (e.g., correlogram) allow statistical tests to be efficiently (and rigorously) applied? Why are such tests more difficult for nonnormalized statistics (e.g., semivariogram)?
5. What is the difference between interpolation and extrapolation? How will the errors of these two different estimates differ? (hint: consider the error bounds for a linear regression).

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CHAPTER 6

LANDSCAPE DISTURBANCE DYNAMICS

Disturbances are integral to ecological systems and affect landscapes across a wide range of scales. The causes of disturbance, the patterns and dynamics they produce, and their ecological consequences are major research topics in landscape ecology. Interest stemmed initially from recognition that disturbance was a conspicuous agent of pattern formation; they create complex landscape mosaics that we readily see. At the same time, disturbances were recognized as a natural agent of change within ecological communities, which contributed to the shift from an equilibrial to nonequilibrial view of the natural world that occurred in the late twentieth century (Wu and Loucks 1995; Perry 2002). Disturbances are key drivers of spatial and temporal heterogeneity because they alter the state and dynamics of a system. In landscape ecology, disturbances are ideal subjects for studies of pattern-process interactions because they both respond to and create landscape pattern.

Disturbance has been defined in numerous ways, and we follow the general definition offered by White and Pickett (1985): "any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability of the physical environment." Natural disturbances include

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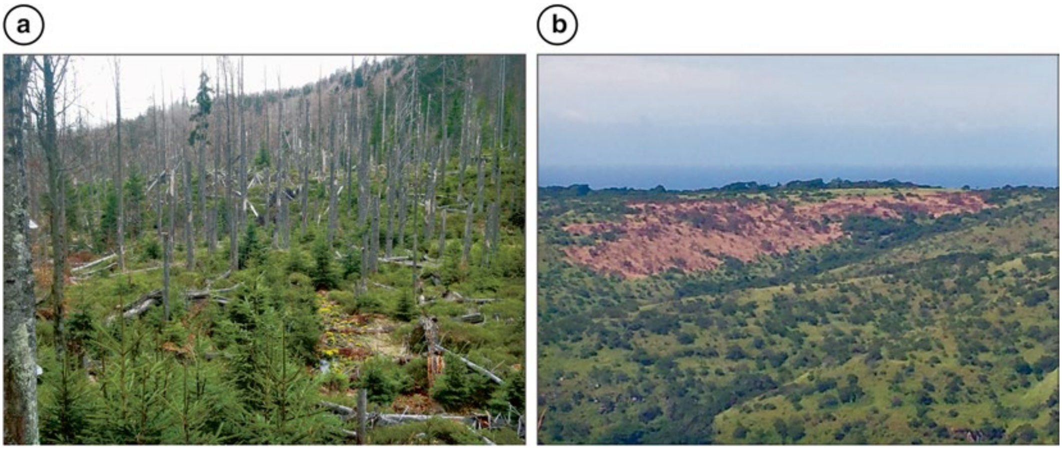


Figure 6.1.

Illustration of two disturbances. (**a**) Standing dead spruce trees in the Bavarian Forest National Park, Germany, were killed by a high-severity bark beetle outbreak; note abundant natural regeneration. Photo by M. G. Turner. (**b**) Fire scar in South Africa in landscape where woody vegetation is expanding. Photo by E. A. H. Smithwick

familiar events such as wildfires, floods, hurricanes, windstorms (e.g., tornadoes, blowdowns), and avalanches (Fig. 6.1). Some ecological systems even require disturbances for maintenance of community structure and ecosystem function (White 1979; Collins et al. 1998). For example, hurricanes contribute to the maintenance of species diversity in many tropical forests, and regular fires may maintain species composition and age mosaics in some landscapes, like prairies and boreal forests. There has been considerable interest in determining whether human activities can be managed to mimic the patterns and effects of natural disturbances and thereby reduce undesirable deleterious effects (e.g., Hunter 1993; Attiwill 1994; Delong and Tanner 1996).

Disturbances produce mosaics of seral stages (Fig. 6.2) that ecologists have long recognized as essential drivers of landscape pattern (e.g., Cooper 1913; Leopold 1933; Watt 1947; Reiners and Lang 1979; White 1979). The literature on *patch dynamics* (Watt 1947; Levin and Paine 1974b; Whittaker and Levin 1977; Pickett and Thompson 1978; Pickett and White 1985; Levin et al. 1993), in which ecological systems were conceptualized as mosaics of patches generated by disturbances, was an important precursor to the more explicit treatment of disturbance in landscape ecology; a concise overview of patch dynamics can be found in Wu and Levin (1994). Patch dynamics implied a relatively distinct spatial pattern but did not establish constraints on patch size, persistence, composition, or geographic location, which may shift through time (Levin and Paine 1974b). In addition, spatial and temporal relationships among patches and with the surrounding matrix were implied. Finally, and perhaps foremost, patch dynamics emphasized change (Fig. 6.2).

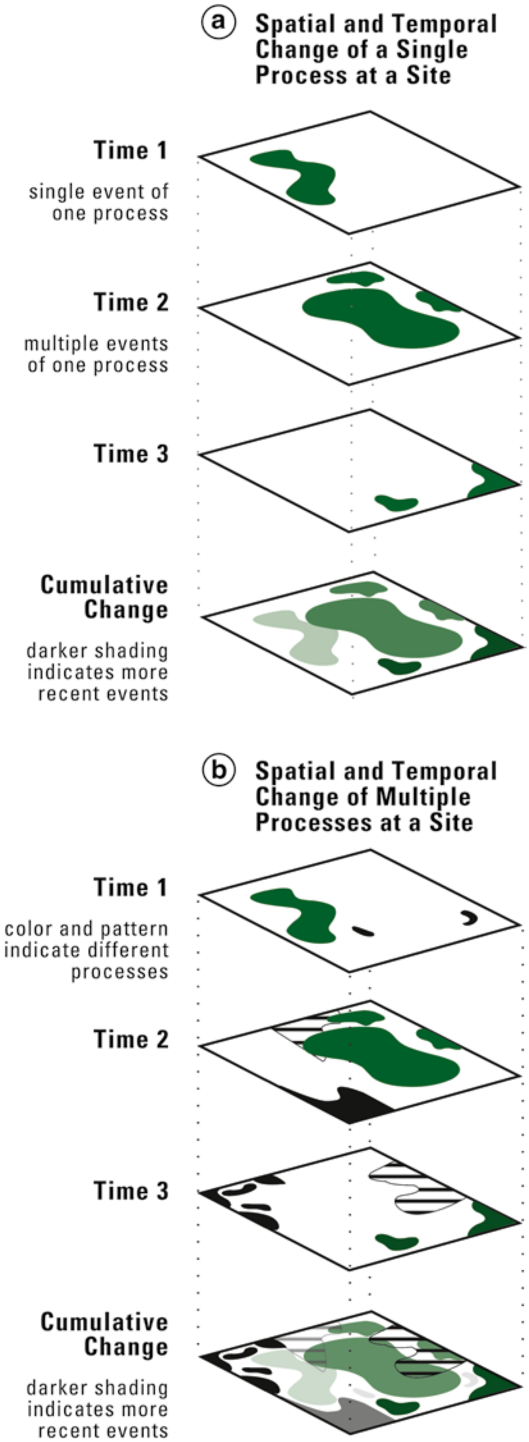


FIGURE 6.2.
Diagrams illustrating patch dynamics. (**a**) Representation of a process that varies in space and time in a hypothetical landscape. Layers represent the site at different points in time, with the patches representing a disturbance impacting different parts of the landscape at each time interval, and the cumulative pattern of the disturbance. Each patch may differ in age, depending on the time it was last disturbed. (**b**) Representation of multiple processes acting on the same landscape through time and cumulatively. When viewed through time, the landscape looks like a changing patchwork in which patches result from disturbances that differ in frequency, intensity, size, and shape.

ADAPTED FROM PARKER AND PICKETT (1998)

Interest in disturbance dynamics has intensified in the twenty-first century (Jentsch 2007; Turner 2010; Peters et al. 2011). Disturbance is a “hot topic” in land and resource management because many disturbance regimes (defined below) seem to be changing due to human activities—especially climate warming. For example, the risk of large fires is increasing in many areas of the world (Westerling et al. 2006; Chapin et al. 2008; Bowman et al. 2009; Girardin et al. 2009), including even the tundra on the North Slope of Alaska (Qui 2009). The Millennium Ecosystem Assessment (2005) reported an increase in the frequency of wildfires as well as floods during the twentieth century in Europe, Asia, Africa, the Americas, and Oceania. Because disturbances can threaten human life and property, often with catastrophic effects on the built environment (e.g., Hurricanes Katrina, which hit New Orleans in 2005, and Sandy, which hit New York in 2012), the consequences of disturbance for human economies and wellbeing are of substantial concern. The potential for disturbances to catalyze major shifts in ecosystems and landscapes, and feedback to global cycles (e.g., carbon cycling), also contributes to the heightened sense of urgency.

In this chapter, we introduce disturbance terminology and concepts then focus on how disturbances interact reciprocally with landscape pattern. We first review how landscape pattern influences disturbance, including work in the emerging field of landscape epidemiology, and then how disturbances create a spatial mosaic in the landscape. We next cover key concepts that require disturbance and succession to be considered jointly and conclude by highlighting disturbance-related questions in contemporary landscape ecology.

DISTURBANCE AND DISTURBANCE REGIMES

Disturbance events happen over relatively short intervals of time: hurricanes or windstorms occur over hours to days, fires occur over hours to months, and volcanoes erupt over periods of days or weeks. In origin, disturbances may be abiotic (e.g., hurricanes, tornadoes, or volcanic eruptions), biotic (e.g., the spread of an exotic pest or pathogen), or some combination of the two (e.g., fires require conditions suitable for ignition and burning, which are abiotic, as well as sources of adequate fuel, which are biotic). Disturbances usually result in “open space,” such as gaps in otherwise continuous vegetation, and they alter levels of resources such as light and nutrients. By producing these open spaces, disturbances create patchiness in a landscape and initiate secondary succession in the disturbed patches. In landscapes subject to large, infrequent disturbances, the spatial pattern imposed by a disturbance event can structure the landscape until the next disturbance occurs. The eruption of Mount St. Helens in 1980 and the Yellowstone fires of 1988 are examples where the large disturbance established the template for species and ecosystem processes in a landscape for decades or centuries to come.

Consequences of disturbance for the biota depend not only on features of the disturbance but also on the state of the system before it was disturbed. For example, tree height influences the extent of uprooting and stem snapping that occurs in forests affected by catastrophic wind. The successional stage of a community when it is disturbed may control the availability of propagules that, in part, shape the composition of the post-disturbance community. The context of the surrounding landscape may also play an important role in post-disturbance succession. Disturbance dynamics and succession are intertwined in their effects on landscape patterns and change, and the successional changes that follow disturbance are main components of our understanding of disturbance in a landscape context.

Ecologists distinguish between a particular disturbance event—like an individual storm or fire—and the *disturbance regime* that characterizes a landscape (e.g., White and Jentsch 2001). The disturbance regime refers to the spatial and temporal dynamics over a longer time period and is described by characteristics such as the spatial distribution of disturbances; disturbance frequency, return interval, and rotation period; and disturbance size, intensity, and severity (Table 6.1). It is important to recognize that definitions of disturbance and disturbance regimes are

TABLE 6.1.
DEFINITIONS OF COMPONENTS OF A DISTURBANCE REGIME, ADAPTED FROM WHITE AND PICKETT (1985) AND TURNER ET AL. (1998b).

Term	Definition
Frequency	Mean or median number of events occurring at an average point per time period, or decimal fraction of events per year; often used for probability of disturbance when expressed as the decimal fraction of events per year
Return interval	Mean or median time between disturbances; the inverse of frequency; variance may also be important, as this influences predictability
Rotation period	Mean time needed to disturb an area equivalent to some study area, which must be explicitly defined
Size	Area disturbed, which can be expressed as mean area per event, area per time period, or percent of some study area per time period
Intensity	Physical energy of the event per area per time (e.g., heat released per area per time period for fire, or wind speed for storms); characteristic of the disturbance rather than the ecological effect
Severity	Effect of the disturbance event on the organism, community, or ecosystem; closely related to intensity, because more intense disturbances generally are more severe
Residuals	Organisms or propagules that survive a disturbance event; also referred to as biotic legacies. Residuals are measure of severity, and thus (at least within one disturbance) an index of intensity

inherently scale dependent (Allen and Starr 1982; Pickett et al. 1989; Turner et al. 1993; Wu and Loucks 1995; White and Jentsch 2001). A particular disturbance may be a disruptive force at fine scales but a stabilizing force at broad scales, where average values over large areas may show minimal change. Thus, as with seemingly all aspects of landscape ecology, one must be cognizant of the scales of the phenomena under consideration.

Comparisons among different disturbances and ecosystems are challenging because so many features, such as the assemblage of species and nature of the disturbance, vary so widely. Developing generality in disturbance ecology requires finding patterns amidst such diversity (White and Jentsch 2001). To support such comparisons, Peters et al. (2011) proposed a new conceptual framework that disaggregates a disturbance event into three measurable components: (1) environmental drivers and their associated characteristics, which interact with (2) initial properties and spatial structure of a given ecological system to determine (3) physical and biological mechanisms that result in a change in system properties (Fig. 6.3). This framework augments a tradition of disturbance research in ecology by focusing explicitly on underpinning mechanisms, disturbance legacies, and influences on future system state (Fig. 6.4, Peters et al. 2011). This disaggregated approach is valuable for landscape studies because it facilitates a more explicit consideration of the multiple contingencies (see Chap. 2) that cause landscapes to respond in different ways.

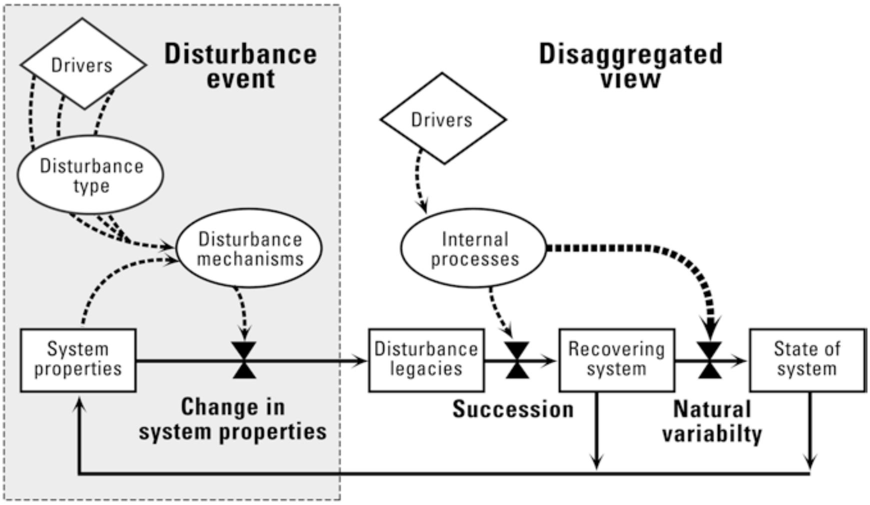
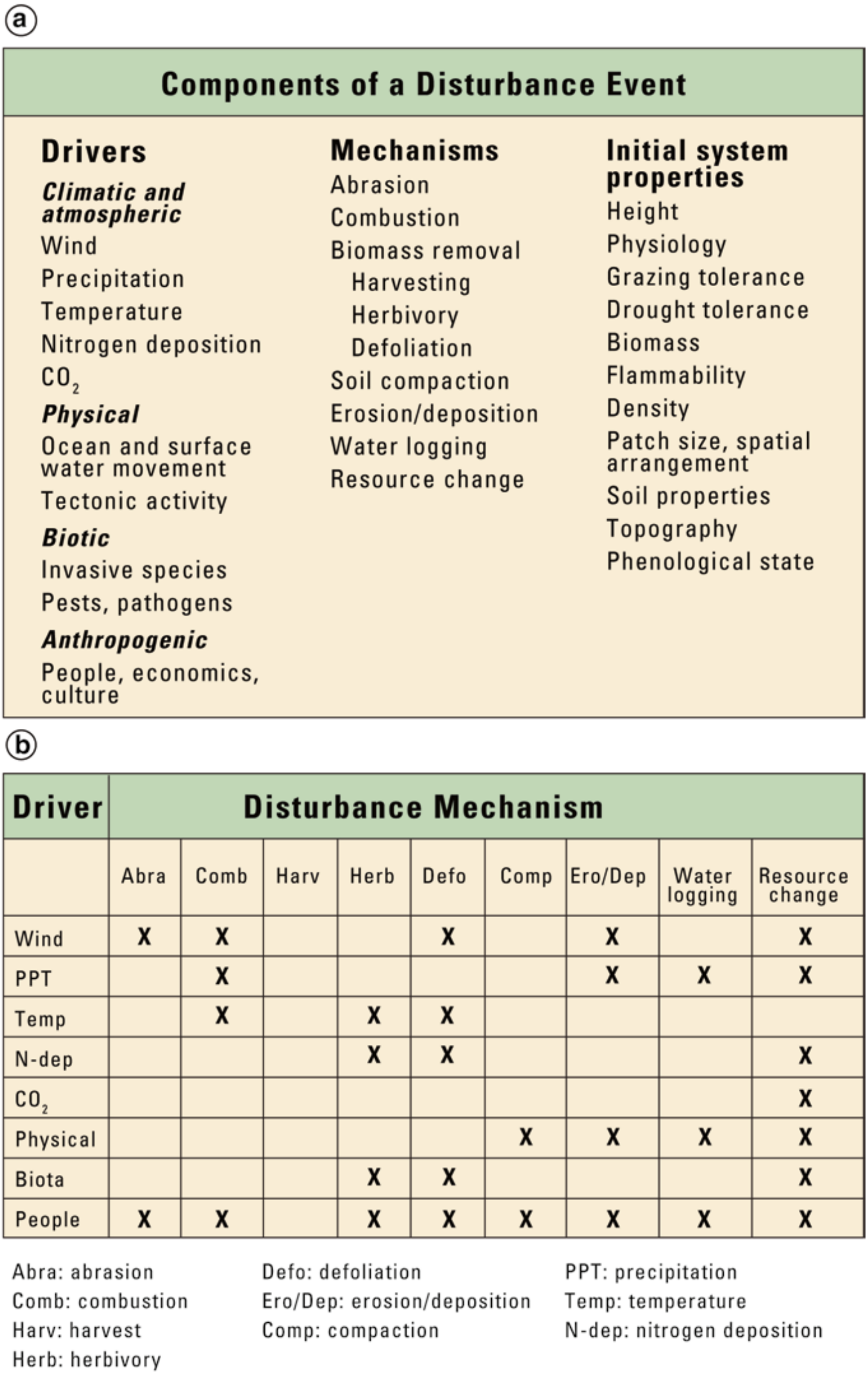


FIGURE 6.3.

Disaggregated view of disturbance. The disturbance event consists of environmental drivers, initial system properties, and physical and biological mechanisms of effect. These result in a disturbed state with legacies that interact with subsequent drivers to influence system response.

ADAPTED FROM PETERS ET AL. (2011)



(a)

Components of a Disturbance Event

Drivers

Climatic and atmospheric
- Wind
- Precipitation
- Temperature
- Nitrogen deposition
- CO_2

Physical
- Ocean and surface water movement
- Tectonic activity

Biotic
- Invasive species
- Pests, pathogens

Anthropogenic
- People, economics, culture

Mechanisms
- Abrasion
- Combustion
- Biomass removal
  - Harvesting
  - Herbivory
  - Defoliation
- Soil compaction
- Erosion/deposition
- Water logging
- Resource change

Initial system properties
- Height
- Physiology
- Grazing tolerance
- Drought tolerance
- Biomass
- Flammability
- Density
- Patch size, spatial arrangement
- Soil properties
- Topography
- Phenological state

(b)

Driver	Disturbance Mechanism								
	Abra	Comb	Harv	Herb	Defo	Comp	Ero/Dep	Water logging	Resource change
Wind	X	X			X		X		X
PPT		X					X	X	X
Temp		X		X	X				
N-dep				X	X				X
CO_2									X
Physical						X	X	X	X
Biota				X	X				X
People	X	X		X	X	X	X	X	X

Abra: abrasion
Comb: combustion
Harv: harvest
Herb: herbivory
Defo: defoliation
Ero/Dep: erosion/deposition
Comp: compaction
PPT: precipitation
Temp: temperature
N-dep: nitrogen deposition

FIGURE 6.4.

Components of a disturbance event (**a**) and the mechanisms that underpin the effects of different disturbance drivers (**b**).

ADAPTED FROM PETERS ET AL. (2011)

EFFECT OF LANDSCAPE HETEROGENEITY ON DISTURBANCE

Landscape pattern can influence disturbance dynamics in two general ways. First, the position of different locations in a landscape can affect susceptibility to a particular disturbance. Second, the configuration of habitats that are and are not susceptible to a particular disturbance can affect how the disturbance spreads through the landscape. We discuss both modes of influence, then consider the emerging area of landscape epidemiology, which bridges these modes and focuses on the role of landscape pattern for disease.

Landscape Position and Vulnerability to Disturbance

Are various spatial locations in the landscape differentially susceptible to disturbance? If so, can we predict which areas are more or less susceptible to particular types of disturbance? *Landscape position* typically refers to the topographic position of a site or group of sites, including relative elevation, landform, slope, and aspect (see Chap. 2). Susceptibility to disturbance at particular landscape positions can be evaluated by comparing the probability or frequency of occurrence of a particular disturbance at many places in a landscape. A variety of field studies have addressed these questions in different types of ecosystem.

Runkle (1985) studied the disturbance regime in cove forests of the Southern Appalachian Mountains and found it was determined by regional and local topographic position. Cove forests occur in sheltered areas at middle elevations and are dominated by mesophytic species (e.g., sugar maple, *Acer saccharum*; yellow buckeye, *Aesculus sylvatica*; yellow birch, *Betula lutea*; American beech, *Fagus grandifolia*; white basswood, *Tilia heterophylla*; and eastern hemlock, *Tsuga canadensis*). Wind-related disturbances were dominated by small disturbance events, resulting in the deaths of one or a few canopy trees (a *forest gap*) at any given location. Interestingly, the rate of repeat disturbance was high. Having initially sampled vegetation in 273 gaps, Runkle revisited these gaps 6–7 years later. New gaps often were forming close to the old gaps such that the changed environmental conditions (e.g., greater sunlight) were maintained, and the process of gap closure was slowed. Thus, landscape position influenced the disturbance regime, and new gap disturbances were more likely to occur in the vicinity of old gaps. Among forest types in the southern Appalachians, cove forests are also those most influenced by human land-use change (Turner et al. 2003a), indicating another interesting influence of landscape position on gap dynamics.

Subsequent research on disturbance in the Appalachian Mountains considered the interaction between landscape position and fire. Using mapped perimeters of fires that burned between 1930 and 2003 in two national parks (Great Smoky Mountains and Shenandoah), Flatley et al. (2011) found that effects of topography on fire varied with climate. Fire was more frequent on dry south-facing aspects, on ridges and at lower elevations. However, this influence of landscape position on fire was weaker during dry years and in Shenandoah, the drier of the two parks. This study illustrates how broad-scale spatial variation in climate, which imposes regional-scale pattern on fire occurrence, can influence the fine-scale interactions of landscape position and fire. Such hierarchical interactions among drivers have long been recognized in disturbance ecology, but interest has resurged in the context of cross-scale interactions driving regional dynamics (discussed below).

Studies in old-growth forests of New England also demonstrated that disturbance acts selectively within a landscape, and sites can be arranged along exposure gradients. Foster (1988a, b) examined a natural disturbance regime characterized by frequent, local events, such as windstorms, pathogens, and lightning strikes, and occasional broad-scale damage by hurricanes and winds. Slope position and aspect controlled the susceptibility of a site to disturbance. For example, hurricane winds that affect the region typically come from the southwest and move eastward, and site susceptibility to hurricane damage was controlled by the degree of exposure to those winds (Fig. 6.5). Following a major hurricane in 1938, exposed southeastern slopes and northwest lakeshores had the greatest damage, and exposed hilltops were also strongly affected. Further work combined analysis of remotely sensed, historical and field data with a meteorological model and a topographic exposure model (Foster and Boose 1992; Boose et al. 1994). Results of these integrated studies demonstrated that forest damage due to hurricanes resulted from characteristics of the storm (e.g., wind directions and maximum gusts), exposure, and the height and composition of the vegetation.

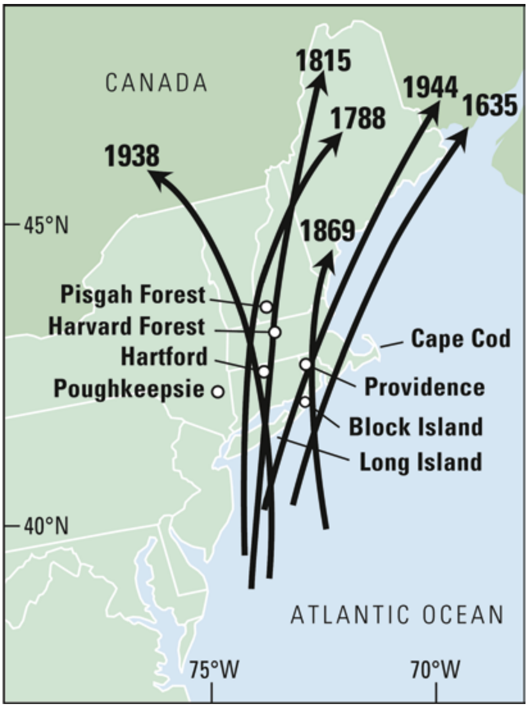


FIGURE 6.5.
Tracks of six severe hurricanes that caused significant forest damage in New England.

ADAPTED FROM BOOSE ET AL. (1994)

Disturbance effects related to exposure have now been reported for many different landscapes. Levels of hurricane damage in Hawaii varied substantially along an elevational gradient (Harrington et al. 1997), and forest stands of similar composition in Minnesota suffered different amounts of windstorm damage based on their location (Dyer and Baird 1997). In coastal temperate rainforest in complex terrain on Kuiu Island, Alaska, long-term spatial patterns of windthrow (Fig. 6.6) were predictable based on slope, elevation, soil stability, and exposure to prevailing winds (Kramer et al. 2001). Twenty percent of the forests of Kuiu Island were affected by catastrophic windthrow (rather than by small gap disturbances), largely concentrated along ridges and valleys that run parallel to prevailing storm winds (Kramer et al. 2001). And in southwest Tasmania, Australia, fires were most likely to burn on flats, ridges, and steep north-facing slopes, and least likely to burn in valleys and on steep south-facing slopes (Wood et al. 2011). Landscape positions that were protected from fire (i.e., topographic fire refugia) were the locations preferentially occupied by rainforest.

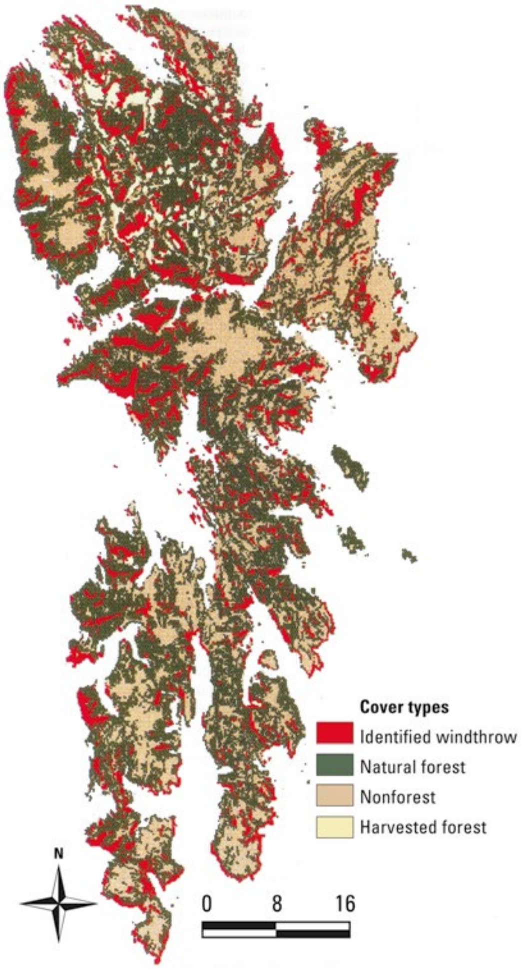


Figure 6.6.

Spatial pattern of windthrow on Kuiu Island, Alaska, along with nonforest area and timber harvest. Patterns were used to determine how slope, elevation, soil, and exposure controlled vulnerability of forests to windthrow.

From Kramer et al. (2001); reproduced with permission

In landscapes subject to fire, landscape position may affect probability of ignition (e.g., Burgan and Hartford 1988; Chou et al. 1993.) In Glacier National Park, Montana (USA), lightning ignitions are greatest on ridgelines and south-facing slopes (Habeck and Mutch 1973). Human influences in the landscape may also affect vulnerability to fire. In the upper midwestern US, Cardille et al. (2001) investigated the relationship between wildfire origin locations and environmental and social factors for >18,000 fires between 1985 and 1995. Fires were more likely to occur in areas of higher human population density and road density. Fire occurrence was also related to size and nearness to roads in boreal forests of Alaska, USA (Calef et al. 2008), but with an interesting twist. Probability of fire was greater near roads because ignitions increased, but fire size was lower within 30–40 km of villages and roads because of fire suppression. Such effects can be surprisingly widespread; Calef et al. (2008) suggested that these human influences on fire pattern affected 31 % of interior Alaska!

Proximity to habitat edges is another way in which landscape position can influence vulnerability to disturbance. In tropical forests of Australasia and Amazonia, Laurance and Curran (2008) observed that fragmented forests were especially vulnerable to wind disturbance along the forest edges. Small forest fragments, with their high perimeter-to-area ratios, were more susceptible, although edge orientation relative to prevailing winds was also important. Land–water margins, another kind of edge, may also influence susceptibility to disturbance. Following a 1998 ice storm in the Adirondack Mountains of north-central New York (USA), Millward et al. (2010) studied damage to forests at the terrestrial–aquatic interface. Ice-storm effects depend on the amount and duration of ice accumulation, wind, and characteristics of the trees and stand. Using field observations and vegetation indices from satellite imagery, Millward et al. (2010) found that forests in riparian zones along large streams (fourth and fifth order) or within 25 m of lake shorelines had significantly more ice-storm damage than did interior forest positions. Furthermore, canopy disturbance declined (by as much as 3.5 times) with movement inland from the land–water margin (Millward et al. 2010). An interesting implication of these findings was that landscape position affected the inputs of wood from the terrestrial to aquatic ecosystem because it influenced susceptibility to ice-storm damage.

Although landscape position effects on disturbance have been reported for many landscapes, there are exceptions; some studies report a weak influence of exposure or find no evidence of significant effects of landscape position on disturbance. In Upper Michigan (USA), Frelich and Lorimer (1991) studied three tracts of old-growth forest in which the disturbance regime included effects of fire, wind, drought, insects, disease, ice storms, and lightning strikes. They tested for differences in the disturbance regime between: upland and lowland sites; aspect classes; slope classes; and the hemlock zone along Lake Superior and the interior forests dominated by sugar maple. Extensive field sampling was conducted, but no significant effects of these factors were observed. The upper Midwest has relatively little topographic relief, and Frelich and Lorimer (1991) suggested that the lack of topographical influence on the disturbance regime in this landscape may reflect the types of windstorms that occur in the Upper Great Lakes Region as compared to those that occur in the Eastern United States. The windstorms that do the greatest damage in the Upper Great Lakes have strong downward components, compared to the horizontal winds of hurricanes; even the Southern Appalachians, where Runkle conducted his work, are influenced by hurricanes, albeit infrequently. In coastal forests in southern Mississippi (USA) where topographic relief is also minimal, stand age rather than landscape position was the best predictor of forest damage following Hurricane Katrina, which made landfall on the central Gulf Coast in 2005 (Kupfer et al. 2008). Uplands in the region are broad and gently sloping, and in that setting, aspect was of modest importance and only in older stands (Kupfer et al. 2008). Studies of the spatial pattern of tornadoes have also demonstrated an absence of physiographic control (Peterson and Pickett 1995). Downbursts (strong downdrafts of air from a thunderstorm or large cumulus cloud that generate an outflow of wind that travels away from the point where it hits the ground) and tornadoes can hit any position in the landscape, resulting in little differentiation among topographic positions.

The extensive 1988 fires in Yellowstone National Park provide another example in which topographic position exerted little influence on susceptibility to disturbance. Topography can influence fire spread, as flames burn more readily uphill than downhill because of the tendency for hot air to move upward. Therefore, leeward slopes often burn with less intensity than windward slopes (Heinselman 1996). However, the burning conditions that occurred in Yellowstone during 1988 were so extreme that slope position, fuel, and even natural firebreaks (e.g., streams, rivers, and even the Grand Canyon of the Yellowstone River) did not impede the fire. Landscape position had little influence on susceptibility to fire because the extreme drought and wind that occurred in Yellowstone during the summer of 1988 overrode fine-scale variation in fuel burning conditions (Turner and Romme 1994).

Synthesis

Can general conclusions be drawn regarding how landscape position influences disturbance? Landscape position influences susceptibility to disturbance when the disturbance itself has a distinct directionality (e.g., hurricane tracks or prevailing winds) such that some locations are usually more exposed than others. In addition, landscape position may influence susceptibility if the disturbance is of moderate intensity, such that its severity is influenced by subtle differences in the landscape. However, if the disturbance itself has no spatial directionality (e.g., downbursts), or it is so intense that its severity is unaffected by differences in the landscape (e.g., high-intensity crown fire), then landscape position does not influence susceptibility to the disturbance.

Effect of Landscape Heterogeneity on the Spread of Disturbance

Understanding effects of landscape heterogeneity on the spread of disturbance was identified by Risser et al. (1984) as a fundamental question in landscape ecology, and this was the theme of the first US landscape ecology symposium, held in 1986 (Turner 1987b). Risser et al. (1984) noted that spatial homogeneity often enhances the spread of a disturbance; consider the spread of pests through agroecosystems, the perpetuation of wildfire or epidemics such as Dutch elm disease. They also noted that other disturbances may be enhanced by landscape heterogeneity; for example, fragmented forests harbor larger populations of deer that disturb surrounding crops or overbrowse native forest species. Landscape heterogeneity also enhances recovery rates by providing refuges for organisms that recolonize disturbed areas. Many studies suggest an interaction between landscape heterogeneity and the spread of disturbance, whether it enhances or retards spread differs among disturbance types (Turner and Bratton 1987; Castello et al. 1995). We'll consider several examples that illustrate aspects of this important interaction.

THEORETICAL DEVELOPMENT

An influential conceptual study by Franklin and Forman (1987) examined the probability of disturbance, e.g., wildfire, windthrow, and pests, as a function of spatial patterns imposed on a forested landscape by clearcutting. Franklin and Forman (1987) explored consequences along a gradient of forest conditions from "primeval" to a completely clearcut landscape. They used simple geometric models (Fig. 6.7) to evaluate how patch size, number of patches, and lengths of edge changed under different cutting patterns; temporal dynamics (e.g., succession) were not considered. Next, implications of these alternative arrangements of forest and cutover lands for disturbances were evaluated. Windthrow susceptibility was assumed to increase with the amount of edge, the isolation of forest in small patches, and with increasing wind fetch. Results of the model demonstrated that windthrow potential would increase initially with forest cutting and continue to increase as forest patches became isolated on all sides (Fig. 6.8a). Wind fetches progressively increased with cutting; after 80 % of the original forest was cleared, windthrow risk to all remaining patches peaked. Susceptibility to both fire ignition and spread, along with risk of particular pest and pathogen outbreaks, were also considered (Fig. 6.8b, c). These simple and insightful models suggested a striking influence of landscape heterogeneity on disturbances, although specific effects varied by disturbance type.

Another conceptual framework for studying effects of landscape heterogeneity on disturbance was developed by Turner et al. (1989a) based on the neutral landscape model approach (see Chap. 3). The landscape was represented as a grid of 10,000 cells containing habitat that either was or was not susceptible to a

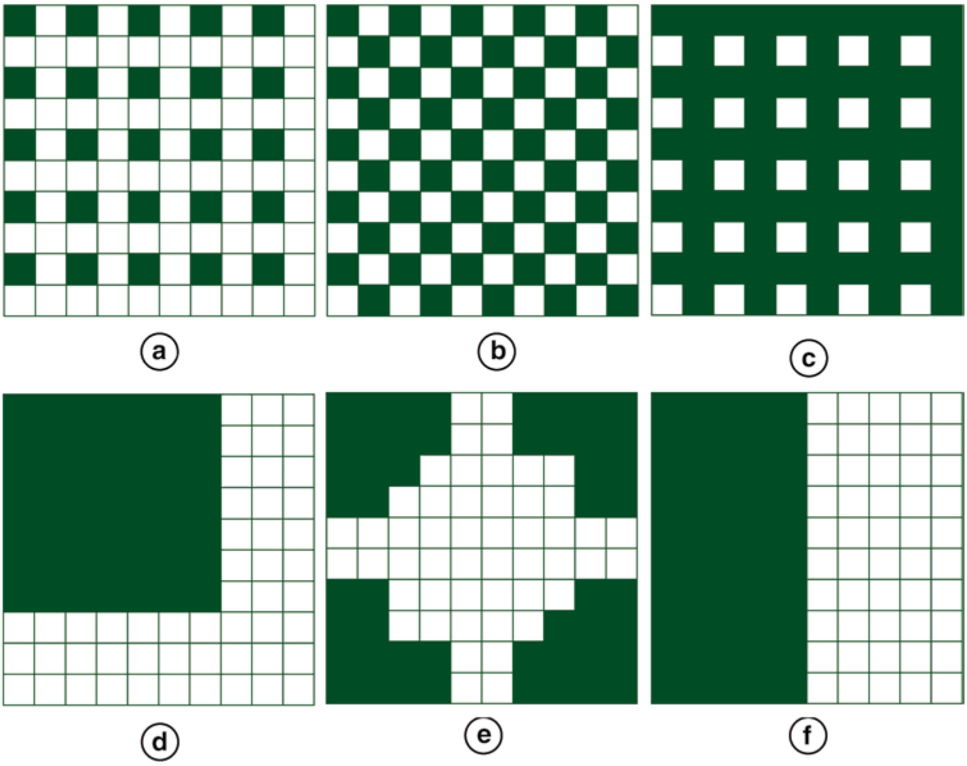


Figure 6.7.

Patterns of clearcutting developed under various models by Franklin and Forman (1987). In (**a–c**), a dispersed cut pattern is used in which the amount of cutover area (*black*) varies but there is a regular distribution across the landscape. In (**d–f**), the cutover area is 50 % but it is arranged as a single nucleus, four-nucleus, or progressive parallel cutting system.

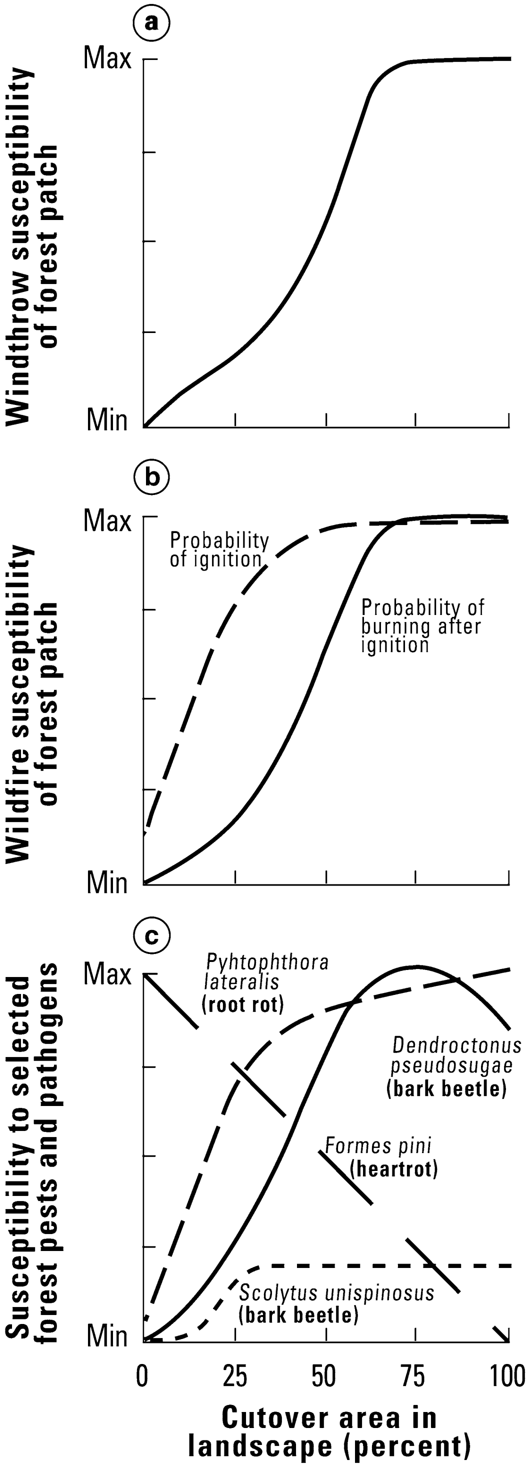
Adapted from Franklin and Forman (1987)

given disturbance. Susceptible habitat was distributed at random and occupied different proportions, p, of the landscape ranging from 0.1 to 0.9. Disturbance was then simulated by two simple parameters: f, the probability of initiation of a new disturbance in a susceptible site, and i, the probability that the disturbance, once initiated, would spread to adjacent sites of the same habitat. Numerous simulations were conducted in which p, i, and f were varied, and the disturbance was allowed to progress until it was extinguished or could not spread any further. Final disturbance extent and landscape patterns were then analyzed. Simulation results demonstrated a qualitative shift in the influence of the landscape on disturbance spread with changes in p (Fig. 6.9). When p for susceptible habitat was less than the critical threshold of connectivity, the percent of available habitat that was disturbed was affected most by f, the probability of new disturbances being initiated, and i had little effect. That is, the fragmentation of susceptible habitat into

FIGURE 6.8.

Predicted susceptibility of forests in the Douglas-fir region to various types of disturbance as a function of the percent of the landscape that is clear cut, as shown by the checkerboard model (see Fig. 6.7b). (**a**) Potential for windthrow in residual forest patches. (**b**) Potential for wildfire ignition and spread. (**c**) Susceptibility to insect and fungus pests.

ADAPTED FROM FRANKLIN AND FORMAN (1987)



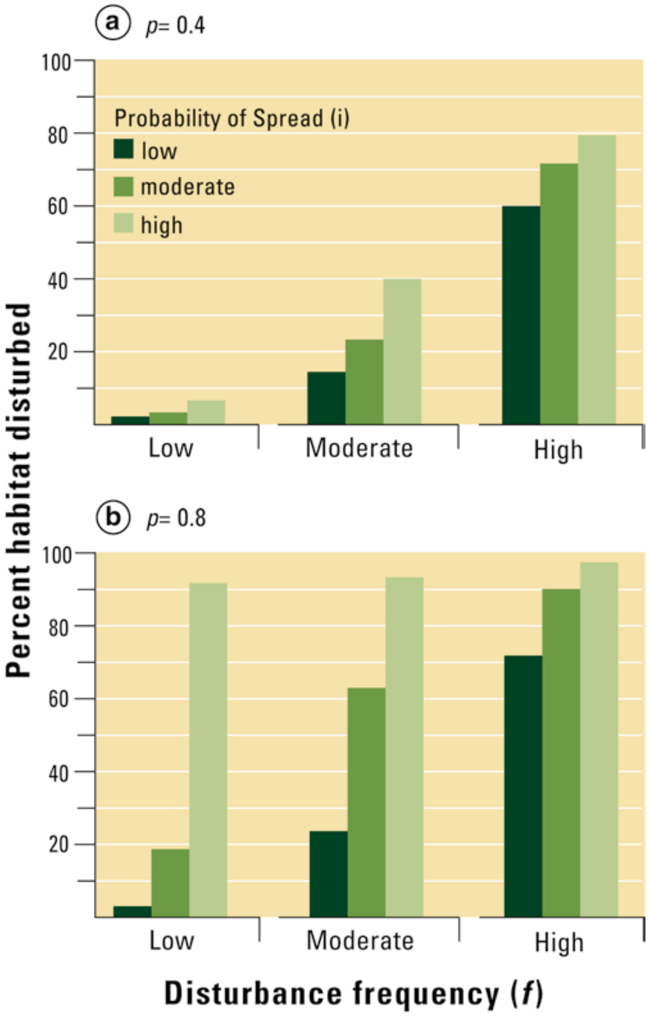


FIGURE 6.9. Simulated percent of susceptible habitat disturbed as a function of the f, the probability of disturbance initiation, and i, the probability of the disturbance spreading to adjacent susceptible sites. (**a**) Initial proportion, p, of the landscape occupied by susceptible habitat is 0.4, below the threshold of connectivity. (**b**) Initial proportion, p, of the landscape occupied by susceptible habitat is 0.8, above the threshold of connectivity.

ADAPTED FROM TURNER ET AL. (1989A)

small, isolated patches prevented disturbance spread across the landscape; the only means for affecting a large proportion of the habitat was to initiate disturbance in many patches. In contrast, once p for susceptible habitat was greater than the critical threshold of connectivity, the probability of spread, i, controlled the percent of habitat that was disturbed. Under these landscape conditions, susceptible habitat formed large, continuous patches, and even a single disturbance could potentially spread across the entire landscape.

Several additional theoretical frameworks consider the role of spatial pattern in disturbance spread. Under the umbrella of cross-scale interactions, Peters et al. (2004b) proposed a conceptual framework for understanding when a series of interactions and feedbacks among fine- and broad-scale processes lead to unexpected "catastrophic" events. This framework emphasizes conditions under which fine-scale processes propagate nonlinearly to have broad-scale impacts, as well as when broad-scale drivers simply overwhelm fine-scale processes. The model links the initiation of

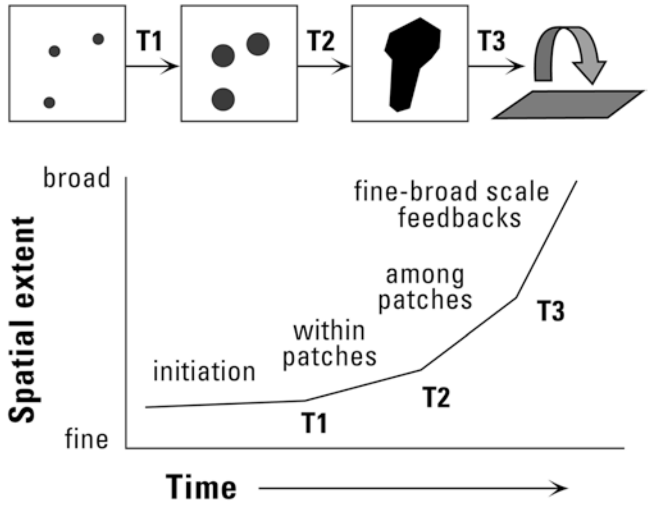


Figure 6.10.
Conceptual framework proposed by Peters et al. (2004b) illustrating a series of spatial nonlinearities and thresholds that may lead to "surprises," or unexpected and even catastrophic events. Event initiation (*T1*) represents the initiation of a disturbance event, which is often stochastic because occurrence, timing and location are difficult to predict. Within-patch expansion of the disturbance (*T2*) depends is contingent on the state of the system and external drivers. Spatial spread of the disturbance (*T3*) is influenced by landscape composition and configuration, and by external drivers

a disturbance event, its within-patch expansion, and its spatial spread among patches (Fig. 6.10). The rate of disturbance spread depends on spatial configuration, connectivity, and flows within and among landscape elements.

The cross-scale interactions framework was used to evaluate dieback of piñon pine (*Pinus edulis*) in northern New Mexico, USA, in part because the dieback could not be attributed to a single cause (Allen 2007). Feedbacks between pattern and process were identified within three different spatial scale domains and included numerous nonlinear, synergistic interactions. Cross-scale interactions were also invoked by Raffa et al. (2008) to explain the series of thresholds that must be surpassed, at multiple scales, for populations of native bark beetles to transition from the endemic to outbreak phase. Another theoretical framework for disturbance that incorporates spatial heterogeneity focuses on self-organized patchiness and catastrophic shifts in ecosystems (e.g., Rietkerk et al. 2004). Regional disturbance regimes play a part in broader considerations of regime shifts, as they may be sensitive indicators of tipping elements (sensu Lenton et al. 2008) that exhibit threshold-like behavior. *Tipping elements* refer to subsystems that can be switched into different states by small perturbations (Lenton et al. 2008). The *tipping point* is the corresponding critical point—in a forcing driver—beyond which the system is altered. As emphasized in hierarchy theory (Allen and Starr 1982; O'Neill et al. 1986) and neutral landscape models (Turner et al. 1989a), these theoretical disturbance frameworks emphasize scale, threshold phenomena, and nonlinear dynamics as key determinants of landscape dynamics. Further, the theoretical frameworks underscore the importance of spatial heterogeneity for understanding the rates and patterns of disturbance.

EMPIRICAL STUDIES

Many studies have focused on the spatial spread of natural disturbances, with pest or pathogen dynamics and fire receiving most attention. There is a rich and varied literature on the subject, and examples discussed here are illustrative and by no means comprehensive.

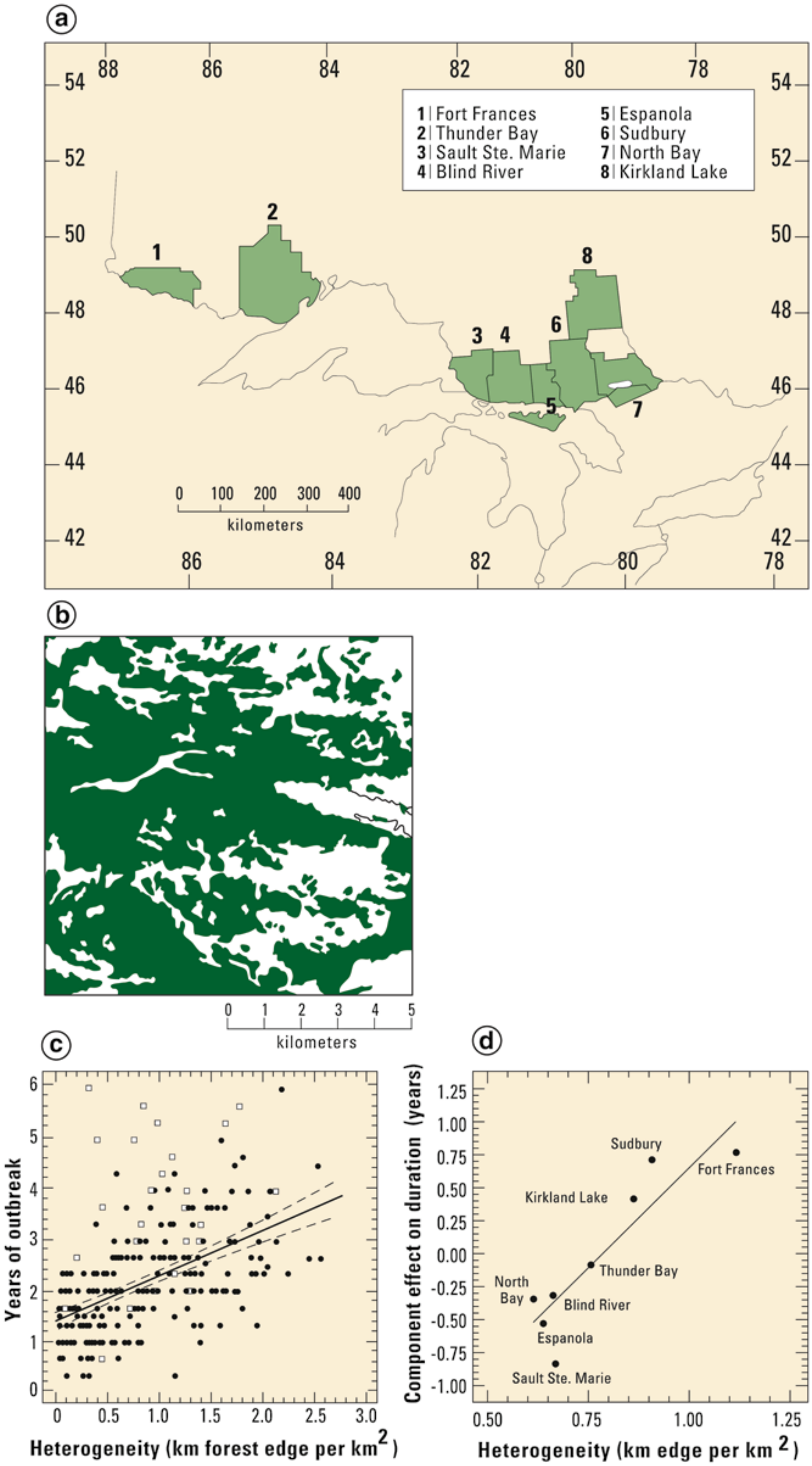
Insect outbreaks. Landscape heterogeneity due to forest fragmentation enhanced outbreaks of the forest tent caterpillar (*Malacosoma disstria*) in northern Ontario, Canada (Roland 1993). Outbreaks in boreal mixedwood forests were of longer duration in areas that had higher landscape heterogeneity resulting from forest clearing and fragmentation. This caterpillar exhibits cyclic population outbreaks and declines with a period of about 10 years, and outbreaks occur in forests that have at least some aspen (*Populus tremuloides*). Following an outbreak, the decline from peak density is associated with high mortality caused by a virus and a parasitic fly. However, the duration of the high-density outbreak phase can vary between 2 and 9 years among regions. Using aerial survey data on the spatial extent of three complete caterpillar outbreak cycles over an area of 26,623 km^2, Roland (1993) calculated mean outbreak duration in 261 townships in eight forest districts and compared this to measures of forest and landscape structure. Results demonstrated a strong effect of forest fragmentation as measured by edge density (km forest edge per km^2). Within townships, each 1 km/km^2 increase in edge density increased duration of the outbreak by 0.92 years. Outbreaks in townships with continuous forest cover lasted only 1–2 years, whereas townships with 2.0–2.5 km/km^2 of edge lasted 4–6 years (Fig. 6.11). Among districts also, the outbreaks were longer in those districts that had high average fragmentation (Fig. 6.11). At both levels, the amount or proportion of

→

FIGURE 6.11.

(**a**) Areas of Ontario, Canada in which duration of forest tent caterpillar outbreaks were related to forest and landscape structure. (**b**) Example from one township (MacPherson Township, North Bay District) showing the distribution of forest (*green*) and nonforested (*white*) land. (**c**) Mean duration of forest tent caterpillar outbreak for 261 townships as a function of edge density for all townships. (**d**) Effect of mean habitat heterogeneity on outbreak duration within the eight forest districts.

REDRAWN FROM ROLAND (1993)


a
88
86
84
82
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54
52
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48
46
44
42
1 Fort Frances
2 Thunder Bay
3 Sault Ste. Marie
4 Blind River
5 Espanola
6 Sudbury
7 North Bay
8 Kirkland Lake
1
2
3
4
5
6
7
8
0 100 200 300 400
kilometers
b
0 1 2 3 4 5
kilometers
c
Years of outbreak
0
1
2
3
4
5
6
0 0.5 1.0 1.5 2.0 2.5 3.0
Heterogeneity (km forest edge per km²)
d
Component effect on duration (years)
1.25
1.00
0.75
0.50
0.25
0.00
-0.25
-0.50
-0.75
-1.00
0.50 0.75 1.00 1.25
Heterogeneity (km edge per km²)
Sudbury
Fort Frances
Kirkland Lake
Thunder Bay
North Bay
Blind River
Espanola
Sault Ste. Marie

aspen was not significant. Roland (1993) suggested several explanations for these results. Broad-scale fragmentation of the forest may affect the interaction between the natural predators on the caterpillar, in that dispersal of the pathogens may be limited by forest fragmentation. In addition, many species of Lepidoptera lay more eggs along the edges of host-plant patches than within the interior, so the forest tent caterpillar abundances may also be greater initially along the forest edges. Warmer microclimatic conditions along the patch edges may also lead to more rapid development of the insect.

In contrast, reconstructions of regional outbreaks of western spruce budworm (*Choristoneura occidentalis*) in the western USA during the past three centuries suggested that landscape heterogeneity decreases the spread of this pest. Swetnam and Lynch (1993) found that the twentieth century had the longest intervals of reduced budworm activity, and an outbreak that occurred through the 1970s and 1980s was unusually severe. Also, budworm infestations and epidemic periods appeared to be most synchronous during the twentieth century, meaning that they were likely to occur simultaneously in many different geographic locations. Budworm infestations develop and spread under conditions of high tree density and connectivity among forest stands, and this was pointed out by interesting variation in the chronologies. For example, a widespread outbreak that occurred during the 1900s–1920s was missing from the Colorado Front Range and the Sangre de Cristo Mountains. Swetnam and Lynch (1993) attributed this absence to the rapid changes that had occurred in the Southern Rocky Mountain mixed conifer forests during this period. Extensive logging and previous fires had reduced conifer densities substantially, and the resulting landscape heterogeneity, in which forests were sparser and less connected, retarded spread of the budworm. Subsequent fire suppression, reduced sheep grazing, and favorable climatic conditions allowed host-tree seedlings to become established, setting the stage for a dramatic future increase in tree density and forest connectivity. During the first part of the century (including the period of the widespread outbreak), these developing forests were less susceptible to budworm outbreaks because they contained few mature trees, and the open stand structure limited dispersal of the budworm. By the 1940s, however, these mixed conifer forests had greater canopy closure, the mature host trees became an important component of stand composition, and the forests were more spatially continuous across the landscape than they had been in presettlement times. Budworm outbreaks subsequently became more widespread and more severe than in earlier periods. Thus, decreased landscape heterogeneity, induced by human activities, resulted in increased spread and synchrony of spruce budworm outbreaks. Regional patterns of budworm outbreak, observed as synchrony among widely dispersed stands, were related to climate control on budworm dynamics—primarily through spring rainfall. However, differences in local patterns resulted especially from land-use history in which stand density, stand age, and landscape pattern could override effects of the broad-scale climatic influences (Swetnam and Lynch 1993).

Landscape heterogeneity also plays a role in bark beetle outbreaks in forest landscapes. During the first decade of the twenty-first century, the frequency, extent, and severity of outbreaks of native bark beetles (Dendroctonae) in western North America have exceeded those documented over the past 125 years (Fig. 6.12). Nearly every coniferous forest type was affected between 1997 and 2010 (Raffa et al. 2008; Meddens et al. 2012). Eruptions of individual species have been larger than previously reported, and temporal synchrony among species appears to be greater. A complex set of controls and feedbacks operate across multiple scales to control bark beetle population dynamics, and numerous thresholds must be exceeded for an outbreak to develop. Included among these is the landscape pattern of forest stands vulnerable to beetle attack. Abundant and well-connected stands of trees that are homogenous in species, age, and genetic structure can enhance the expansion of an outbreak, whereas more heterogeneous forest patterns can impede spread (Raffa et al. 2008). In western Canada, management practices resulted in forests in which nearly 70 % of the lodgepole pine (*Pinus contorta*) was >80 years old and in size classes vulnerable to mountain pine beetle (*Dendroctonus ponderosae*). This host abundance was three times the amount of susceptible pine observed in the previous century (Taylor and Carroll 2004). Along with environmental conditions (e.g., warmer climate increasing overwinter beetle survival and shortening the life cycle) that have become more favorable to bark beetles, the structure and connectivity of the forests increased the likelihood of beetle outbreaks spreading across the landscape.

Fire. The role of landscape heterogeneity in controlling fire spread has been explored in a variety of systems. In some coniferous forests, landscape heterogeneity in forest age classes can affect fire spread (e.g., Givnish 1981; Foster 1983; Foster and King 1986). If flammability is related to stand age (e.g., by affecting fuels), the spatial distribution of old and young stands may enhance or constrain fire spread. In California, fires in chaparral burned well in old stands, but diminished in patches of younger vegetation (Minnich 1983). There may be critical thresholds in environmental constraints that determine whether or not landscape heterogeneity will influence the spread of crown fire (Turner and Romme 1994; Renkin and Despain 1992). Landscape pattern may have little influence on crown-fire behavior when burning conditions are extreme (Turner and Romme 1994; Fig. 6.13). Under conditions of extreme drought and high winds, all fuels across the landscape become highly susceptible to burning and may render the occurrence of large stand-replacing fires inevitable (Fryer and Johnson 1988; Johnson 1992; Bessie and Johnson 1995).

For fire, the degree to which landscape factors affect fire spread or severity depends on the relative importance of *top-down* versus *bottom-up* factors (Littell et al. 2009). Top-down forces include the strong influence of regional climate and

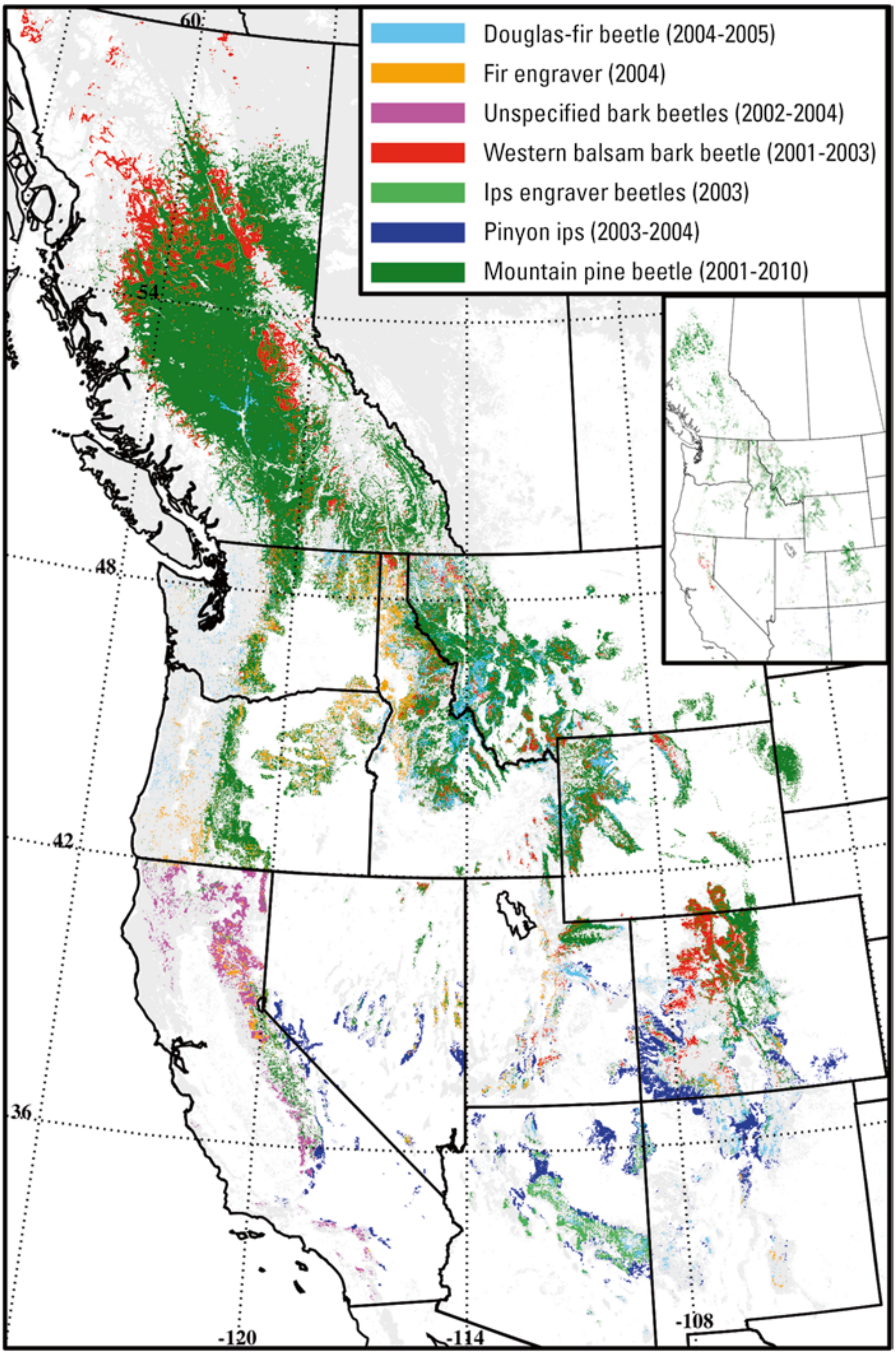

Figure 6.12.

Major bark beetle outbreaks in the western United States and British Columbia, Canada between 2001 and 2010. Light shading depicts all forested areas.

Reprinted with permission from Meddens et al. (2012)

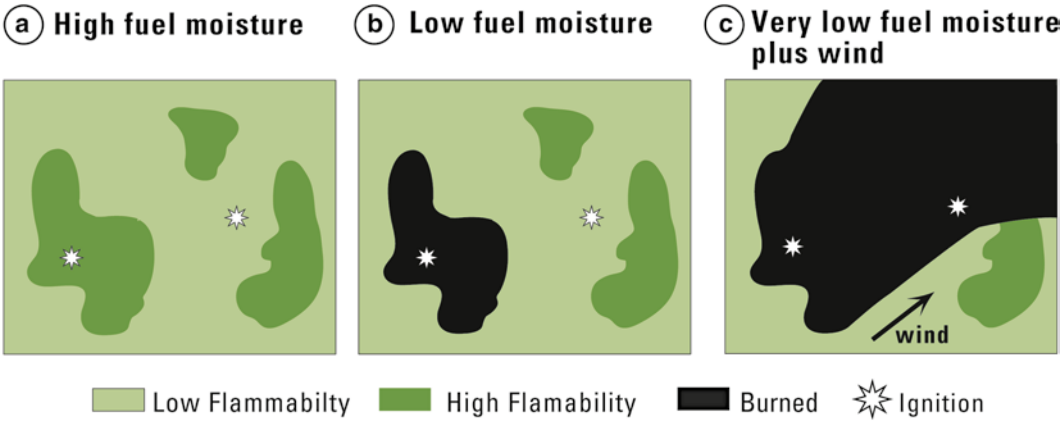

FIGURE 6.13.

Interaction between hypothesized thresholds in both meteorological conditions and landscape pattern that interact to produce large crown fires. (**a**) If fuel moisture is high, lightning strikes (*stars*) are unlikely to initiate a fire, even if the strike occurs in highly flammable forest (*dark green*). Landscape pattern does not control fire spread. (**b**) If fuel moisture is low, but burning conditions are not extreme, then crown fires (*black*) are likely to be constrained by the spatial distribution of highly flammable patches in the landscape. (**c**) If fuel moisture is extremely low and there are strong winds, crown fires (*black*) are likely to burn through a variety of fuel types. Under these conditions, the patterning of more flammable stands does not constrain fire spread.

ADAPTED FROM TURNER AND ROMME (1994)

regional geomorphology, which affect large areas and influence fire frequency, size, and severity. Bottom-up forces include local factors, such as stand and landscape structure and topography, which are more spatially variable. In general, bottom-up factors relate to the amount and connectivity of fuel in the landscape. Evaluating top-down and bottom-up controls on fire regimes has received much recent attention (e.g., Heyerdahl et al. 2001; Mermoz et al. 2005; Meyn et al. 2007; Morgan et al. 2008; Parisien et al. 2011; Parks et al. 2012). All fire regimes are influenced by both, but regimes characterized historically by infrequent, high-severity fire typically have strong top-down forcing and may show little influence of bottom-up factors (e.g., the 1988 Yellowstone Fires; Turner et al. 1994b). In contrast, regimes characterized by frequent, low-severity fire typically have strong bottom-up forcing and are more responsive to landscape pattern. For example, drier low-elevation and mid-montane forests in western North America historically experienced frequent fires that maintained an open forest structure. Such fires are very responsive to local fuel availability, and antecedent weather conditions that produce lush herbaceous growth are often associated with big fires. For example, large fires at lower elevations in southeastern Arizona, USA, occurred when antecedent conditions remained wet until just before the fire season (Crimmins and Comrie 2004). In forests adapted to a low-severity fire regime, changes in forest structure, such as increased tree density from fire-exclusion, can increase wildfire spread and severity (Schoennagel et al. 2004; Miller et al. 2009). Some landscapes are characterized by mixed-severity fire regimes that contain areas of both high- and low-severity fire and are governed by a delicate balance between top-down and bottom-up controls (Perry et al. 2011). Indeed, the importance of mixed-severity fire is being recognized in more and more landscapes. The degree to which fire-prone landscapes can be managed to achieve desired management goals remains a hot topic in landscape ecology and natural resource management (Stephens et al. 2013; Moritz et al. 2014).

Synthesis. Given the wide range of studies on the subject, can we generalize about whether landscape heterogeneity does or does not enhance the spread of disturbance? The answer depends on whether the disturbance spreads *within* the same cover type, such as the spread of a species-specific parasite through a forest, or whether it crosses boundaries and spreads *between* different cover types (Turner et al. 1989a). If the disturbance spreads within the same cover type, then greater landscape heterogeneity should retard the spread of disturbance. This was observed in the spruce budworm and bark beetle examples (Swetnam and Lynch 1993; Raffa et al. 2008), and the spread of fires under moderate burning conditions (Turner and Romme 1994). If the disturbance spreads between cover types or is otherwise enhanced by edge effects, then increased landscape heterogeneity should enhance the spread of the disturbance. This was observed in the forest tent caterpillar (Roland 1993) and windthrow (Franklin and Forman 1987) examples. Other studies suggest circumstances in which landscape heterogeneity does not influence disturbance spread because the broad-scale abiotic controls override the local landscape controls; large infrequent crown fires (Turner and Romme 1994) and tornadoes (Peterson and Pickett 1995; Frelich and Lorimer 1991) provide examples. In sum, there are important controls at multiple scales, and the role of landscape heterogeneity in enhancing or retarding disturbance spread strongly depends on whether other thresholds have been exceeded (e.g., Peters et al. 2004a, b; Allen 2007; Raffa et al. 2008). Clearly, landscape heterogeneity and disturbance remains an active and vibrant area of landscape ecological research, both in theory development and empirical study.

Landscape Epidemiology

Landscape epidemiology is an emerging interdisciplinary related to disturbance spread. *Epidemiology* deals with the spread of a disease from individual to individual through a population and predicts outcomes, such as rate of spread and the proportion of the population affected by the disease. *Spatial epidemiology* is the study of spatial variation in disease risk or incidence, and while many studies focus on the spatial dynamics of disease, the role of landscape structure has only recently received study (Ostfeld et al. 2005). *Landscape epidemiology* aims to identify the factors that influence the spatial spread of diseases among subpopulations of human, animal, or plant hosts (Plantegenest et al. 2007; Reisen 2010; Meentemeyer et al. 2012). Because research in landscape epidemiology comes from studies on a wide range of host taxa, relevant studies are also found under other names (e.g., *landscape pathology*, which focuses on tree diseases, is the intersection of forest pathology and landscape ecology; Holdenrieder et al. 2004).

How might landscape heterogeneity affect disease? Landscape structure (and thus land-use change) may affect disease dynamics through influences on abiotic conditions (such as changing edge conditions or environmental gradients) and on species interactions that contribute to disease prevalence or spread (Ostfeld et al. 2005). Landscape structure becomes important for disease risk or incidence if it influences disease vectors, reservoirs, or pathogens.

Parallels between the spread of natural disturbances and diseases have been apparent for some time. For example, O'Neill et al. (1992) developed a model derived from epidemiology theory and applied it to the spread of disturbance in a landscape. Results demonstrated that the spatial pattern of susceptible sites, particularly as related to their connectivity, could determine the total extent of a single disturbance event. Spatial models of disease spread proved useful for understanding and predicting the spread of pests, pathogens, and disease (e.g., Hohn et al. 1993; Liebold et al. 1993; Castello et al. 1995; Nicholson and Mather 1996). Since then, a growing number of empirical studies have elucidated ways in which landscape heterogeneity affects disease incidence and spread. These studies seek to relate the spatial patterns of disease dynamics to attributes of the landscape, much as ecologists relate spatial patterns of natural disturbance to landscape structure. Studies in landscape epidemiology often consider both the influence of landscape position (i.e., related to host landscape pattern) on disease incidence and the influence of landscape structure (i.e., connectivity) on disease spread.

Landscape epidemiology studies have revealed effects of landscape structure on the incidence of many different pests and diseases, especially if pattern affects pathogen dispersal vectors. Landscape position is important for passive transport of pathogens by wind or water, and landscape elements may be barriers or conduits for spread. For example, windbreaks surrounding vegetable gardens in Provence, southeastern France, acted as barriers that slowed the dispersal of vectors of cucumber mosaic virus (Marrou et al. 1979). In contrast, road and creek corridors were conduits that increased the dispersal of spores of *Phytophthora lateralis*, a nonnative root pathogen that causes "root rot" in Port Orford cedar (*Chamaecyparis lawsoniana*) in the Pacific Northwest (USA) (Jules et al. 2002). Spores were unintentionally transported in mud on vehicles traveling the road network, from which they dispersed along the stream network. Because the spores disperse by gravity, landscape position also played a role: uninfected trees also were more vulnerable when located downslope of infected trees, rather than upslope.

The recent dieback of oaks (*Quercus* spp.) known as sudden oak death (SOD) provides another example of landscape influence on disease. Oak trees have died along hundreds of kilometers of the California coast, and a non-native pathogen, *Phytophthora ramorum*, was identified as the cause. The pathogen causes rapid development of cankers that girdle the tree and cause its death. Analyses of the spatial pattern of oak mortality revealed that proximity to forest edge was most important, and this effect was explained by the abundance of understorey hosts in edge environment (Kelly and Meentemeyer 2002). Increased diversity of other host species that are less competent appears to dilute transmission of the disease by competent hosts; disease risk was lower in sites with higher species diversity (Haas et al. 2011). However, landscape connectivity also plays a role. Ellis et al. (2010a) tested the importance of connectivity relative to other environmental variables in determining the spatial distribution of SOD. Among several measures evaluated, a connectivity term calculated with effective distances (Euclidean distance modified to account for how landscape structure can influence spread) performed best. Environmental variables were relatively more important, but connectivity still mattered (Ellis et al. 2010a, b).

In agricultural landscapes, crop damage due to pests and pathogens may depend on composition and configuration of the surrounding landscape. For example, an increase in landscape complexity in 1.5-km diameter landscapes around canola fields was associated with decreased damage by the canola pollen beetle (*Meligethes aeneus*) and increased parasitism of the pest by parasitoids (Thies et al. 2003). Patterns in the surrounding landscape also influenced the abundance of *Delphacodes kuscheli*, an insect known to transmit Maize Rough Dwarf Virus to maize fields in Argentina (Grilli 2010). The composition, configuration, and stability of patches in the surrounding landscape can influence potential pathogen reservoirs and the abundance of alternative hosts, which can affect damage levels on a focal species.

Landscape patterns related to habitat fragmentation and edges also play a role in the epidemiology of human diseases. Globally, the trend of emerging infectious diseases appears to be associated with ecotones, especially edges that are created or modified by humans (Despommier et al. 2007). Among emerging diseases, Lyme disease has been studied most thoroughly, and landscape structure has emerged as a particularly strong driver. Lyme disease is the most frequently reported vector-borne disease in the United States and Europe (Killilea et al. 2008, and references therein). In North America, Lyme disease is caused by *Borrelia burgdorferi*, a spirochete bacterium, which is vectored by ticks of the genus *Ixodes*. Many birds and small mammals are potential reservoir hosts, but the dominant hosts are rodents (e.g., white-footed mice, *Peromyscus leucopus*). Humans become infected when bitten by a tick that was infected previously when feeding on an infected host (Killilea et al. 2008). Incidence of Lyme disease requires reservoir hosts, ticks, and humans to occur in close proximity, and thus the factors that influence tick presence and abundance, the mammalian and avian community, and the presence of humans may all influence disease prevalence.

Landscape patterns influence the prevalence of Lyme disease in the tick populations, with fragmented forest landscapes (i.e., many small forest fragments and a lot of forest-edge habitat) having higher entomological risk (Allan et al. 2003; Brownstein et al. 2005). Tick density and infection prevalence were both higher in forest fragments that were smaller and more isolated. The elevated level of tick infection was linked, in turn, to changes in composition of the vertebrate community. The vertebrate community becomes less diverse as forests become fragmented, with many species disappearing in small forest patches. The species-poor communities have abundant white-footed mice, which is the most competent host for the disease-causing bacterium (LoGiudice et al. 2003). As new host species are added to a depauperate community, the tick infection rate declines (LoGiudice et al. 2003) because the nonmouse hosts are much less competent. Thus, the higher species diversity in the community of hosts dilutes the effects of the white-footed mice. Surprisingly, while the patterns of the host reservoir and tick infection rates are linked clearly to landscape structure, the patterns of Lyme disease incidence in humans remain to be explained (Brownstein et al. 2005; Killilea et al. 2008). However, the strong influence of total forest and forest edge on tick infection rates suggests that landscape designs that reduce the amount of forest edge could help mitigate Lyme disease risk (Jackson et al. 2006).

A landscape connection has been suggested for the spillover of bat viruses to human populations, including the 2014 outbreak of Ebola in West Africa. Much like the example discussed above for the series of thresholds that must be passed for endemic bark beetle populations to irrupt, a hierarchy of conditions is required for people to become infected by viruses that originate in bats (Plowright et al. 2015). At the landscape level, land-use changes that increase interaction between species, leading to more contact between human and bat populations, are associated with increased likelihood of transmission to humans. In areas of central and northwest Bangladesh with recurring outbreaks of Nipah virus, which is transmitted by fruit bats (*Pteropus giganteus*, also called flying foxes), landscape composition and structure influences disease incidence (Hahn et al. 2014a). Villages in the "Nipah Belt" have forests that are more fragmented than forest surrounding other comparable villages that had no reported outbreaks of Nipah virus. Detailed studies of habitat selection of the fruit bats, along with characteristics of the villages and landscape, are helping to develop land management strategies that can protect fruit bats while minimizing risks to public health (Hahn et al. 2014a, b).

The conceptual framework of landscape ecology promises to complement understanding of disease emergence and spatial dynamics in ways that may help to reduce the incidence of troubling diseases (Plantegenest et al. 2007). A landscape perspective on disease management also can contribute to sustainable land-use patterns (Holdenrieder et al. 2004). Ongoing studies in landscape epidemiology will reveal which site factors and landscape patterns affect susceptibility to a wide range of diseases in plants, animals, and people.

EFFECTS OF DISTURBANCE ON LANDSCAPE HETEROGENEITY

Studies of how disturbances respond to landscape patterns have produced a rich understanding of one side of the reciprocal pattern-process relationship. We now turn to the other side this relationship: the role of disturbances in generating landscape patterns.

The Disturbance-Generated Mosaic

When a disturbance occurs, it does not act uniformly throughout a landscape. Rather, disturbances create very complex patterns across the landscape in which the disturbance may affect some areas but not others, and severity of the disturbance often varies considerably within the affected area. When we talk about the *disturbance mosaic*, or the spatial pattern created by disturbance, we refer to the spatial distribution of disturbance severities across the landscape. For example, the 1988 fires in Yellowstone National Park created a complex pattern of burned and unburned areas across the landscape (Fig. 6.14), and the burned areas themselves

FIGURE 6.14.

The landscape mosaic created by the 1988 Yellowstone fires as observed from the air in October 1988, shortly after the fires had been naturally extinguished

(PHOTO BY M. G. TURNER)

had widely variable severities within them (Christensen et al. 1989; Turner et al. 1994a). Even very large crown fires rarely consume an entire forest because variations in wind, topography, vegetation, and time of burning result in a mosaic of burn severities (effects of fire on the ecosystem) and islands of unburned vegetation across the landscape. Complex mosaic patterns of disturbance have been described in many systems, including even benthic communities in the Antarctic for which ice scouring is the key disturbance (Teixido et al. 2007).

Many studies have made excellent use of landscape metrics to describe disturbance-created landscape patterns. In such studies, the proportion of the landscape that is disturbed or in different disturbance-severity categories is determined, and landscape composition and configuration metrics are computed. For example, the number, size and shape complexity of forest patches were used to describe changes in forest fragmentation following a mountain pine beetle epidemic in British Columbia, Canada (Coops et al. 2010). Understanding disturbance-driven changes in variability per se also can be insightful (Fraterrigo and Rusak 2008). Variability can be quantified using either absolute measures (e.g., standard deviation), which tend to increase with the mean; or relative measures (e.g., coefficient of variation), which are normalized and more comparable among different properties. Measures of variability can be highly sensitive and independent of the mean, thereby capturing effects that may be obscured by averaging. For example, spatial variability in forest stand structure (measured by the coefficient of variation in stand density among stands of similar age) *increased* following fire in the Yellowstone landscape, then slowly declined for the next 175–200 years (Kashian et al. 2005b). In contrast, variability in a range of physical, chemical, and biological properties (also measured by the coefficient of variation) *decreased* with flooding in a river–floodplain landscape (Thomaz et al. 2007). Thus, disturbances can both amplify and dampen variability, and not surprisingly, effects of disturbance on variability can differ with scale (Fraterrigo and Rusak 2008). Increased variability has been suggested as a leading indicator of qualitative changes arising from disturbance (e.g., van Nes and Scheffer 2005; Brock and Carpenter 2006). Quantifying and tracking changes in disturbance-induced variability through time may lead to new ecological insights about pattern-process dynamics as well as improved methods for anticipating big changes.

Considerable interest in large, infrequent disturbances (Turner et al. 1997a; Turner and Dale 1998) emerged following a number of natural disturbances that received considerable attention from the ecological research community and the general public (e.g., the eruption of Mount St. Helens in 1980, the 1988 Yellowstone fires, the 1993 floods in the Midwestern US, and Hurricanes Hugo in 1989 and Andrew in 1992). Foster et al. (1998) compared landscape patterns produced by different large, infrequent forest disturbances (Fig. 6.15). Here, we draw upon the synthesis by Foster et al. (1998) and more recent empirical studies to illustrate the variety of landscape patterns generated by wind, floods, and fires.

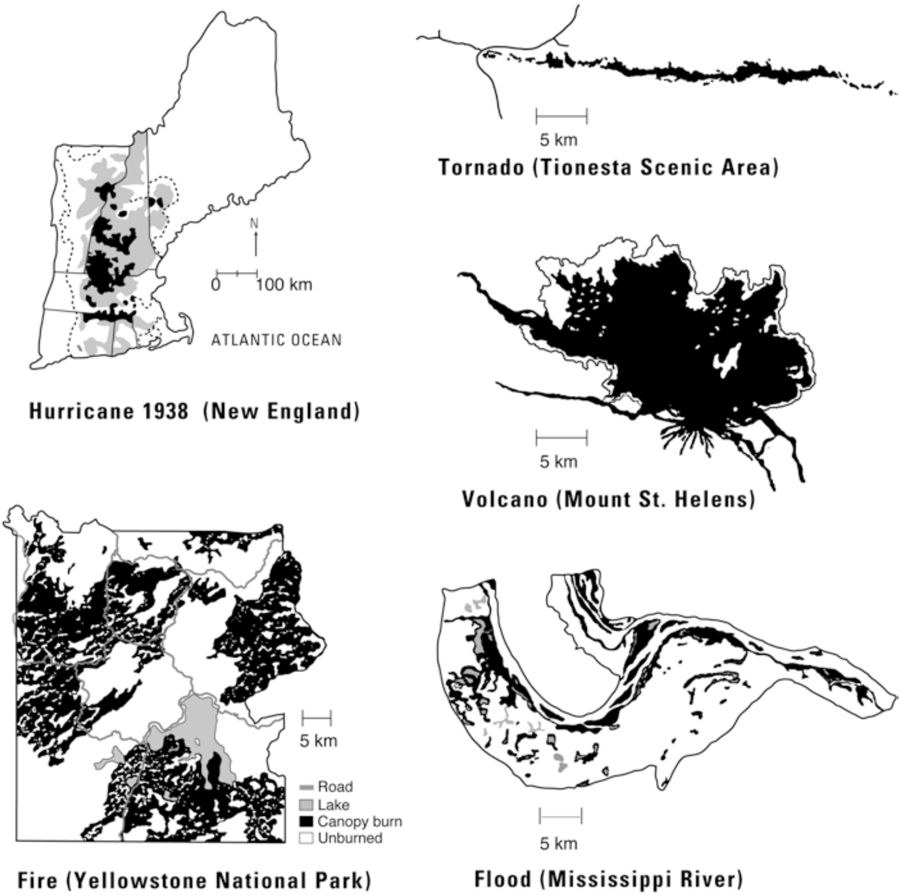

FIGURE 6.15.
Landscape and regional-scale patterns of forest disturbance resulting from five contrasting large infrequent disturbances: the 1938 hurricane in New England, the Yellowstone fires of 1988, the eruption of Mount St. Helens in 1980, the tornado at the Tionesta Scenic Area in Pennsylvania, and floods in the Mississippi River in 1993. The areas of greatest disturbance are shown in *black*. Lesser disturbance severity is shown in *gray*.

FROM FOSTER ET AL. (1998)

Hurricanes produce a patchwork of forest age and height structure, uproot mounds and downed boles, standing broken snags, and leaning and damaged trees (Fig. 6.15; Foster 1988a; Foster et al. 1998). Severe windstorms, such as the extensive windstorm that affected 150,000 ha in the Boundary Waters Canoe Area (BWCA) in northern Minnesota, USA, in 1999 have similar effects (Lain et al. 2008). In addition, increased accumulations of fine woody debris and leaves may increase the likelihood of fire occurring in the same area (Patterson and Foster

1990; Paine et al. 1998; Woodall and Nagel 2007). In contrast to hurricanes, tornadoes are relatively small and short-lived, although they are violent and unpredictable. A grouping of tornadoes that affected Pennsylvania, Ohio, New York and Ontario in 1985 illustrates the landscape pattern of severe tornadoes (Peterson and Pickett 1995). Tracks of the tornadoes were oriented eastward and northeastward, resulting in more than 800 km of tornado damage. Path widths averaged 500 m and ranged from <200 to >2750 m. The damage patterns of tornadoes are remarkable for the sharpness of the edges between intact forest and completely windthrown areas (Peterson and Pickett 1995). Hurricanes, blowdowns, and tornadoes are extremes in the gradient of size and severity of wind damage; however, all storm types have a gradient of intensities and severities and vary in the spatial extent of damage (Foster et al. 1998).

Seasonal flooding is a natural process in many river systems, and the suppression of floods is actually a major disturbance to most river–floodplain ecosystems. However, exceptional floods may create extensive and heterogeneous disturbance patterns in the riverine landscape. A case study of extreme flooding in the Sabie River, Kruger National Park (South Africa) provides an example (Parsons et al. 2005). High-resolution aerial photographs were used to quantify patch mosaics in different geomorphological channel types before and after flooding, and to determine whether flooding changed the extent of patches, generated new patch types, removed existing patch type, or altered patch shape or aggregation. The flood left a heterogeneous imprint of biotic and abiotic patches in the river landscape, and the effects on the mosaic different among channel types (Fig. 6.16; Parsons et al. 2005). In turn, these patterns influenced the riparian vegetation response. In large river–floodplain landscapes, flood duration varies spatially across the floodplain with land elevation and is a critical influence on survival of biotic populations (Sparks et al. 1998).

Many studies have quantified spatial patterns of fire throughout the world, and interest in understanding fire patterns has grown as the annual area burned continues to increase. An excellent synthesis of patterns and scales of heterogeneity created by large fires in US landscapes is provided by Keane et al. (2008). Large fires usually occur during moderate to extreme drought, often with high winds (i.e., strong top-down forcing). In northern and montane forest landscapes, large infrequent fires account for <3 % of all fires but more than 95 % of the land area burned (Johnson 1992). Large fires create a mosaic of patches that vary in size, shape, and severity, as illustrated by 1988 Yellowstone fires (Christensen et al. 1989; Turner et al. 1994a). Large fires may contain more high-severity fire within their perimeter as compared to small fires, but the extent of high-severity fire is often less than people expect. For example, consider burn severity and patch metrics for 25 small (<3000 ha) and 11 large (>10,000 ha) fires in the northern Rocky Mountains (Keane et al. 2008). There were few statistically significant differences in proportions of burned area for small and large fires, and even the large fires averaged only 25 % of the area in high-severity fire. However, spatial patterns differed (Keane et al. 2008).

FIGURE 6.16.

Pre- (**a**) and post-flood (**b**) views of the Sabie River landscape. The riparian forest can colonize substrate across the entire width of the channel, as shown in the upper pre-flood photo.

FROM PARSONS ET AL. (2005)

In large fires, patches were fewer and larger, had less edge, and were more regular in shape than in small fires (Table 6.2). Landscapes of mixed-severity regimes have a wider range of spatial and temporal variability in the disturbance mosaic, but they typically include many small and few large high-severity patches (Perry et al. 2011). The complexity of the burn mosaic means that even areas of high-severity fire may

TABLE 6.2.
SELECTED LANDSCAPE METRICS DESCRIBING THE POSTFIRE LANDSCAPE MOSAIC OF BURN SEVERITIES FOR 25 SMALL (<3300 HA) AND 11 LARGE (>10,000 HA) FIRES IN THE NORTHERN ROCKY MOUNTAINS.

Attribute	Small fires	Large fires	*P* value
Proportion (p) of fire by burn-severity class			
Unburned	0.21	0.15	0.105
Low	0.25	0.21	0.273
Moderate-low	0.18	0.18	0.273
Moderate-high	0.19	0.20	0.702
High	0.16	0.25	0.052
Patch metrics			
Patch density (patches 100 ha^{-1}	91	67	0.003
Landscape shape index (unitless)	23	103	0.0001
Edge density (m ha^{-1})	306	247	0.0005

DATA WERE DERIVED FROM LANDSAT TM (THEMATIC MAPPER) IMAGERY, FIRE SEVERITY WAS CHARACTERIZED USING THE DIFFERENCED NORMALIZED BURN RATIO, AND LANDSCAPE METRICS WERE COMPUTED IN FRAGSTATS.

Source: KEANE ET AL. (2008)

contain a substantial amount of internal edge and be surprisingly close to unburned or less severely burned areas (e.g., Turner et al. 1994a; Donato et al. 2009).

Analyses of disturbance patterns can provide insight into the processes controlling disturbance, and they may also be sensitive indicators of changing disturbance regimes. Increased access to remotely sensed imagery and algorithms for fire-severity mapping has facilitated such studies. For example, Collins et al. (2007) used satellite data and the differenced Normalized Burn Ratio (dNBR) to describe landscape patterns of fire severity in two fires Sierra Nevada wilderness areas (USA). The dNBR index is calculated by comparing pre-fire and post-fire remotely sensed imagery (Key and Benson 2006) then categorizing values by burn-severity class. They then used FRAGSTATS to compute the area-weighted mean patch size for each burn-severity category. The two fires had similar proportions of burned and unburned, but the two fires produced very different disturbance mosaics. One fire had larger patch sizes of high-severity fire, whereas the other fire had larger patch sizes of low-severity fire within the fire perimeter (Collins et al. 2007). Weather was more important in explaining patterns in the higher-severity fire, and vegetation more important for the lower severity fire (Collins et al. 2007). In a southern African savanna, fire patterns were compared in areas that differed in dominant land-use, and landscape metrics were computed from annual maps (1971–2001) that included burned areas (Hudak et al. 2004). In the savanna, more burning increased patch size, size variability, shape complexity, suggesting that fire promoted landscape heterogeneity (Hudak et al. 2004).

Landscape patterns generated by human activities have also been well studied, especially patterns resulting from forest harvest strategies (e.g., Franklin and Forman 1987; Li et al. 1993; Gustafson and Crow 1996). Detecting differences in landscape mosaics resulting from forest harvesting vs. natural disturbances have been a primary research focus. Delong and Tanner (1996) compared the spatial characteristics of landscapes in British Columbia subjected to regularly dispersed 60–100 ha clearcuts with the historic patterns generated by wildfire. Wildfires created a more complex landscape mosaic that included a greater range of patch sizes and more complex disturbance boundaries. In addition, individual wildfires were often >500 ha in size, but unburned forest patches remained within the perimeters of the fire (Delong and Tanner 1996). Harvesting created more fragmented habitat than fire in western Canada (Wang and Cumming 2010) and Greater Yellowstone, USA (Tinker et al. 2003). In the Yellowstone region, timber harvesting on the Targhee National Forest produced landscape patterns in which the number of patches was three times greater and patch sizes were 70 % smaller than patterns produced from wildfires (Tinker et al. 2003). However, contrasting results were observed for forests in northwestern Ontario, Canada, where Gluck and Rempel (1996) observed that patches in clearcut landscapes were larger in size and more irregular in shape than patches in a wildfire landscape.

There has been much discussion in the literature about developing management strategies that mimic natural disturbances in a particular landscape (Hunter 1993; Attiwill 1994), with the implicit assumption that ecological processes will be better maintained in this way. Runkle (1991) suggested that temperate deciduous forest should be harvested in a pattern that mimics small treefall gaps, whereas Hunter (1993) recognized that boreal forests would require very large clearcuts if they were to imitate the size and arrangement of boreal fires. Improved understanding is needed of the nature and dynamics of disturbance mosaics in a wide variety of landscapes and how these differ from those generated by human disturbances. We re-visit this topic later in this chapter when discussing the historic range of variability.

SYNTHESIS

The key take-home message regarding disturbance-created landscape patterns is that they are remarkably diverse and complex. This general conclusion comes from studies of many different disturbances in a wide range of landscapes. Disturbance is the key driver of spatial pattern in many landscapes, producing a mosaic of undisturbed and disturbed patches that vary in size, severity, shape, and arrangement. In turn, succession makes this mosaic pattern dynamic.

Disturbance and Spatial Patterns of Succession

Disturbance and succession are inextricably linked when we consider landscape dynamics. Ecologists have been trying to understand and predict vegetation change since the very beginnings of the discipline, and excellent treatments of the development of successional concepts can be found in Glenn-Lewin et al. (1992) and Walker and del Moral (2003), along with a wonderful synthesis and historical perspective by Christensen (2014). Recovery following disturbance can be very sensitive to spatial pattern created by disturbance and is strongly influenced by the spatial pattern of biotic residuals that are left behind.

The legacies and residuals that remain after the disturbance play a big role in post-disturbance succession (Turner and Dale 1998; Swanson et al. 2011; Donato et al. 2012). Ecological legacies of disturbance have both biological and physical components. *Biotic legacies*, or *residuals*, refer to the types, quantities, and patterns of organisms and biotic structures that persist from the pre-disturbance ecosystem. For example, residuals may include surviving individuals, standing dead trees, vegetative tissue that can regenerate, seed banks, litter, carcasses, and microbial and fungal soil organisms. These organic structures create habitat for surviving and colonizing organisms following disturbances (Swanson et al. 2011). *Abiotic legacies* are physical modifications of the environment that may result from the disturbance, such as mudslides or slope failures, lava flows, or movements of rocks or boulders in streams. Understanding the nature of the disturbance mosaic and the factors controlling these landscape patterns is essential for predicting ecosystem dynamics and vegetation development in disturbance-prone landscapes (Swanson et al. 2011; Donato et al. 2012).

A thorough understanding of succession must include understanding of how successional processes vary with respect to disturbance intensity, size, and frequency (van der Maarl 1993; Turner et al. 1998a; White and Jentsch 2001). Investigations into mechanisms of plant succession following fire and other disturbances often emphasized the autecology and life history attributes of individual plants and species (e.g., Connell and Slatyer 1977; Noble and Slatyer 1980; Peet and Christensen 1980; Pickett et al. 1987a, b; Halpern 1988, 1989). These studies also demonstrated that species responses may vary with different kinds and severities of disturbance and with the larger spatial and temporal context of the disturbance (also see Pickett 1976; Finegan 1984; Glenn and Collins 1992). Patch size, heterogeneity, and distance from undisturbed sites can affect species in a manner dependent on their life history characteristics (Denslow 1980a, b; Hartshorn 1980; Miller 1982; Malanson 1984; Green 1989; Peterson and Carson 1996).

Life history traits related to the ability of the pre-disturbance populations to resist or tolerate a particular type of disturbance interact with disturbance intensity to influence the species composition of residuals. For example, mobility and degree of adaptation to flooding were critical in determining the effects of the 1993 Mississippi River floods on taxonomic and functional groups of organisms in the midwestern USA (Sparks et al. 1998). Virtually all individuals of tree species that could not tolerate the anoxic conditions that developed under extended soil saturation during the growing season died (Sparks et al. 1998). In contrast, some species of aquatic plants survived by growing upward into the lighted zone as the flood rose, and a rare species of false aster (*Boltonia decurrens*) that requires fresh mudflats for seed germination increased dramatically (Smith et al. 1998).

Residual plants that reestablish vegetatively following disturbance often achieve large sizes more quickly than those that start from seed, and species with abundant or larger residual seeds have a head start on those that must disperse into the disturbed area from the surroundings. One example comes from the regeneration of a large forest windthrow. In 1985, a powerful tornado created a 400-ha area of windthrow in the old-growth hemlock-northern hardwoods forest of the Tionesta Scenic Area in northwest Pennsylvania. During initial revegetation following the windthrow event, thickets of surviving advance regeneration of *Fagus grandifolia* and *Acer pensylvanicum* had a substantial size advantage over individuals that germinated after the disturbance, and that size advantage has been maintained (Peterson and Pickett 1995). These thickets of advance regeneration severely inhibited local colonization by *Betula alleghaniensis*, which is abundant in other areas of the blowdown with fewer residuals (Peterson and Pickett 1995). The relationship between disturbance severity and species-regeneration mechanisms (e.g., vegetative reproduction or seed dispersal and establishment) was nicely presented by Roberts (2004; Fig. 6.17). This framework emphasizes herbaceous vegetation, but it explicitly considers the relative abundance of biotic legacies and their role in post-disturbance succession.

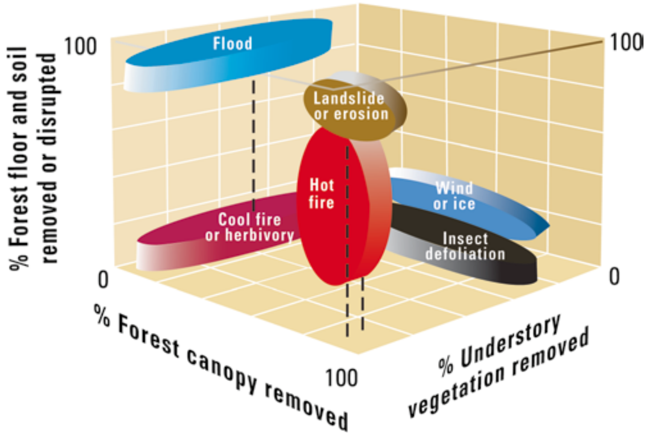

FIGURE 6.17.

Conceptual model of disturbance severity with each of three major vertical layers in the forest ecosystem on a separate axis. Labeled polygons relate the ranges in condition on these three axes to common natural disturbances in North American forests.

ADAPTED FROM ROBERTS (2004)

An interesting landscape question is whether, or under what conditions, the size of a disturbance patch influences successional rates or pathways. Following the 1988 fires in Yellowstone, vegetation sampling during the first 5 years after fire demonstrated significant effects of patch size and burn severity on early succession (Turner et al. 1997b, 2003b). These effects diminished through time as the herbaceous plant populations continued to fill in the burned areas, and the effects of soils and climate on plant communities became more pronounced (Turner 2010). However, an enduring legacy of the burn-severity mosaic was the spatial variability in postfire lodgepole pine density across the landscape (Kashian et al. 2005b; Turner 2010), which will persist for decades to centuries.

Why might disturbance size be important for succession? Disturbance-induced changes in the biophysical environment are subject to edge effects related to disturbance size (Turner et al. 1998b). The centers of large, disturbed patches are likely to experience quite different physical conditions than small patches or disturbed areas near intact vegetation. In tropical moist forest, for example, larger gaps experienced higher air temperatures, lower humidity, higher wind speeds, and reduced soil moisture (Denslow 1987). However, it is on the availability of propagules where disturbance size may exert its strongest effect (Turner et al. 1998b).

The availability of propagules is a fundamental determinant of successional patterns (Clements 1915; Pickett et al. 1987a, b) and one that can be especially sensitive to the combination of high intensity and large size (Turner et al. 1998b). In small disturbed areas, the surrounding intact community is likely to provide sufficient propagules for succession, even if biotic residuals are few. However, the density of propagule inputs from the surrounding undisturbed area into a disturbed area decreases with distance (Johnson 1992; Nepstad et al. 1990; da Silva et al. 1996), so the proportion of disturbed area beyond the zone of high propagule input decreases as disturbance size increases. If dispersal from outside the disturbed area is important, then the size, shape, and configuration of disturbed patches will influence propagule availability and thus vegetation composition. Distance from the edge of the disturbed patch, which is controlled in part by patch size, has a particularly strong effect (McClanahan 1986; Bergeron and Dansereau 1993; Galipeau et al. 1997). For example, spatial patterns of fire severity, and especially those of high-severity burn, were key determinants of postfire shift from coniferous to deciduous forest in boreal forests of interior Alaska (Barrett et al. 2011).

SYNTHESIS

Effects of the landscape disturbance mosaic on succession must consider disturbance severity, which influences the abundance of residuals (Turner et al. 1998b). Turner et al. (1998b) suggested that succession will be relatively predictable following disturbances of any size when residuals are abundant and the effects of local environmental attributes (e.g., nutrient availability, soil texture, and soil moisture) are considered (Fig. 6.18). Spatial effects (disturbance size, shape, and arrangement) become increasingly important when residuals are few or sparse and the disturbance is large; under these conditions, colonization and hence succession become slower and more difficult to predict (Fig. 6.18). Furthermore, if the frequency of large, high-intensity disturbances increases such that residuals decrease in abundance or change in composition with successive disturbance events, successional pathways may shift qualitatively (Fig. 6.18). Landscape context may interact with species life history traits to initiate different successional trajectories within similar abiotic environments because of local variation in disturbance intensity or availability of plant propagules (Glenn-Lewin and van der Maarel 1992; Fastie

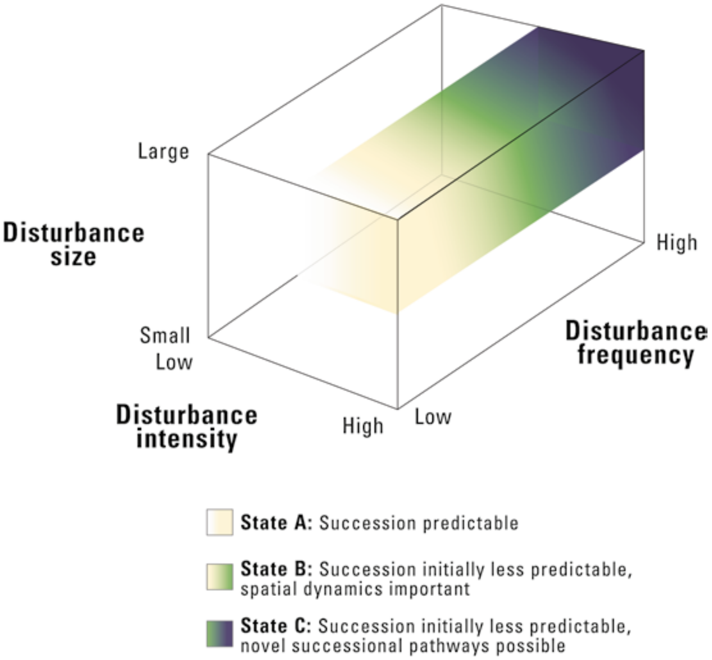

Figure 6.18.

Conceptual state-space diagram for succession following disturbances varying in size, intensity, and frequency. Succession is more predictable and spatial attributes of the disturbance are less important whenever disturbance intensity is low (such that residuals are abundant) or disturbances are small (*state A*). Succession is initially less predictable and determined by disturbance size, shape, and configuration when disturbance intensity is high (such that residuals are scarce) and disturbances are large (*states B and C*). Successional pathways may be qualitatively altered if high-intensity, large disturbance increase in frequency (*state C*).

Adapted from Turner et al. (1998b)

1995; Baker and Walford 1995). Predicting successional trajectories is important but difficult because so many contingent factors come into play.

INTEGRATING DISTURBANCE AND SUCCESSION IN SPACE AND TIME

Modeling Disturbance and Succession

Spatial interactions and long time scales make it challenging to understand how disturbance and succession interact to generate landscape dynamics (He and Mladenoff 1999; Mladenoff and Baker 1999). Integrated models of disturbance and succession are useful tools that can reveal trends and dynamics in landscapes that cannot be easily observed empirically (see review by Seidl et al. 2011b). For example, Peterson (2002) wanted to understand how *ecological memory* (i.e., the degree to which an ecological process is shaped by its past modifications of a landscape) influences landscape dynamics. Empirical data that spanned multiple disturbance cycles over hundreds of years were not available, so he developed a model that linked fire and vegetation regrowth to predict landscape pattern dynamics. Simulation results revealed that the persistence of spatial patterns depended on the degree to which previous fires influenced the spread of subsequent fires (Peterson 2002). Increased ecological memory established a feedback between fire spread and landscape pattern; in the absence of this feedback, fire-shaped landscape patterns but did not themselves respond to landscape patterns. This example illustrates use of an integrated model for addressing a general conceptual question on theoretical landscapes. Integrated models are also very useful for addressing questions of broad-scale disturbances or global change in real landscape settings.

One example of a widely used model of disturbance and succession is LANDIS, developed originally for a 500,000-ha landscape in northern Wisconsin, USA (Mladenoff et al. 1996; He and Mladenoff 1999; Mladenoff 2004). LANDIS operates on landscapes mapped as grid cells that contain different age classes of different tree species. The model represents landscape heterogeneity caused by spatial variation in environmental conditions and disturbance rates, as well as the effects of past human uses in the landscape. Multiple disturbance types are simulated, including fire, windthrow, and forest harvest, and succession is represented at the species level. Successional dynamics are based on life history attributes (e.g., shade tolerance, disturbance susceptibility, vegetative reproduction, time to sexual maturity, longevity) of up to 30 species, and spatial processes such as seed dispersal are included.

An early application of LANDIS was initialized with current landscape pattern for a forest landscape in the upper Midwest, USA, and used to simulate landscape dynamics for 500 years with fire as the only disturbance (He and Mladenoff 1999). Results demonstrated that even when the presettlement disturbance regime was reestablished, some species, such as hemlock, yellow birch, oak and pine, did not recover their presettlement proportions of the forest community for 100–500 years. They also found that landscape recovery could be detected at broad spatial scales as composition of the forest communities became more differentiated on different land types. Interestingly, the landscape showed greater alteration on the more mesic landforms in which disturbances were infrequent but severe, as compared to the more xeric landforms in which disturbance was more frequent but less severe. Similar results have been observed in other systems (Gardner et al. 1996; Turner et al. 1998a).

Development of LANDIS has continued, and LANDIS-II introduced variable time steps, which allow greater flexibility in the model environment (Scheller et al. 2007). One application of the model nicely demonstrated the value of spatial simulation modeling to explore multiple influences on regional landscape dynamics. LANDIS-II was used to study interactions between climate change and disturbance on forest expansion along a prairie–forest ecotone in south-central Minnesota, USA (Berland et al. 2011). The study considered the potential influences of long-term climate changes, including the Little Ice Age; initial tree population distributions, seed dispersal, edaphic factors, and firebreaks; fire regimes; and human influences. Simulations ran for 600 years and covered a 25,000-km^2 landscape. Simulated forest expansion was very sensitive to initial conditions, and multiple pathways could produce similar patterns and rates of forest expansion (Berland et al. 2011). The relationship between fire and fuels (i.e., between disturbance and succession) was required to predict forest dynamics consistent with the historical record. Notably, this result is consistent with the general feedbacks between fire and vegetation that emerged from the more theoretical modeling approach used by Peterson (2002).

It is important to remember that these modeling approaches are not used deterministically to predict what will happen with specific individual events. Models such as LANDIS and Fire-BGC (Keane et al. 1996a, b) incorporate feedbacks among species, disturbance, and environmental variability and are valuable tools for examining complex interactions of species and disturbance over large areas and long time periods.

Disturbance and the Historic Range of Variability

An obvious consequence of the interaction between disturbance and succession is that landscape patterns constantly change. However, dynamic landscape patterns posed a practical problem for ecologists and landscape managers. If landscapes were not static, identifying reference conditions that indicated a functional or resilient landscape became problematic—a single snapshot could not represent the dynamic range of conditions that might be observed through time (e.g., Fig. 6.2). There was also recognition that keeping landscapes in a fixed state was neither possible nor desirable. The concept of the *historical range of variability* (*HRV*) was introduced as a means for incorporating spatial and temporal variability in ecosystem management (Cissel et al. 1994; Landres et al. 1999). The HRV refers to the variation of historical ecosystem characteristics and processes over time and space scales that are appropriate for a particular management application (Keane et al. 2009). The idea was that the recent history of a landscape, which would presumably include a broad envelope of conditions (e.g., disturbed area, patch-size distributions of different communities successional stages) that support landscape resilience, could be a yardstick for evaluating ecological status and change (Keane et al. 2009). The HRV could also provide guidance to forest managers who wished to emulate natural disturbance regimes (Long 2009).

Once again, scale is paramount: the HRV must be quantified for a particular space–time domain. Response variables will be entirely different when quantified for 100 vs. 500 years, or over a landscape of 1000 ha vs. 1,000,000 ha. Quantifying the HRV requires a time series of spatially explicit historical data. These data may come from digital maps of landscape characteristics obtained for multiple time periods, or from spatial simulation models run over a reference time period. Of course, not every attribute of a landscape can be quantified for its HRV. Response variables should be measurable across the relevant spatial and temporal extent; representative of the patterns, processes, and characteristics that govern landscape dynamics; and appropriate for the relevant management application (Keane et al. 2009). An excellent overview of these methods and the advantages and limitations of the HRV is provided by Keane et al. (2009).

Once quantified, the HRV can be used to guide landscape management. Actions such as forest harvesting can be scheduled such that responses of interest (e.g., amount and patch-size distributions of old and young forest) remain within the bounds of the HRV. This approach is frequently termed *emulating natural disturbance regimes* (*ENDR*), and it emerged as a dominant paradigm of forest management in North America (Long 2009). ENDR refers to management strategies and practices, at appropriate spatial and temporal scales, with the goals of producing forest ecosystems that are structurally and functionally similar to the ecosystems that would result from natural disturbances (Perera et al. 2004; Long 2009).

The HRV and ENDR concepts embody the shift from a static to dynamic view of landscapes. They are intuitively appealing concepts that have provided tremendous guidance for land management, but data limitations and scale dependence remain nontrivial issues. It is also difficult to decide exactly which characteristics of the disturbance regime and HRV are to be conserved in the future or emulated by land management. Whether current society will find the historic disturbance regime acceptable is also an issue (Thompson et al. 2009). Perhaps the greatest challenge, however, is that fundamental changes in environmental drivers (e.g., climate warming) may limit the ability of past landscape dynamics to guide the future.

Concepts of Landscape Equilibrium

Questions of whether or not equilibrium could be detected on landscapes subject to disturbance, and how large a landscape must be to incorporate a given disturbance regimes, have been important themes in landscape ecology (Shugart and West 1981; Romme 1982; Baker 1989a). Because these ideas were part of a fundamental shift in ecological thinking and are so relevant for basic and applied ecology, we review development of theses concepts as they apply to landscape ecology in some depth. Controversy regarding equilibrium stemmed in part from inconsistent definitions and criteria, and in part from disagreement about whether it was valid to define the existence of an equilibrium state at all (Turner et al. 1993). DeAngelis and Waterhouse (1987) provided an excellent review of the treatment of these concepts in ecological models, and Grimm and Wissel (1997) offer an informative user's guide to terminology.

The notion of equilibrium in ecological systems has inspired a long history of interest and controversy in ecology (e.g., Egerton 1973; Bormann and Likens 1979; Connell and Sousa 1983; Wiens 1984; DeAngelis and Waterhouse 1987). Pickett et al. (1994:159) identified equilibrium as one of few overarching paradigms in ecology, and one of the oldest and most pervasive, which affect the dialog between observable phenomena and conceptual constructs in all the more specialized areas of ecology. Among six tenets of this paradigm identified by Pickett et al. (1994) was that the system was essentially free of disturbance—a problematic assumption given the ubiquitous nature of disturbance and succession. The shift in ecology from an equilibrium view of nature to the nonequilibrium paradigm occurred gradually throughout the twentieth century. In the nonequilibrium paradigm, ecological systems are thought to be open, to be regulated by both intrinsic and extrinsic factors, to lack a stable point equilibrium, to be nondeterministic, to incorporate disturbance, and to admit human influence. Equilibrium might appear, but only at certain spatial and temporal scales (Pickett et al. 1994). Concepts of equilibrium are confounded by problems of scale, and landscapes can exhibit a suite of dynamics of which equilibrium is but one (Turner et al. 1993).

Equilibrium points can be precisely defined mathematically, but equilibrium and stability are not well defined when applied to real ecological systems (DeAngelis and Waterhouse 1987). Properties used to evaluate equilibrium fall into two general categories: *persistence* (i.e., nonextinction, or presence), and *constancy* (i.e., no change or minimal fluctuation in numbers, densities, or relative proportions). Persistence can be applied to all species or to the presence of all stand-age classes or successional stages in a landscape (e.g., Romme 1982). Constancy may refer to the number of species (e.g., MacArthur and Wilson 1967), the density of individual species (e.g., May 1973), the standing crop of biomass (e.g., Bormann and Likens 1979; Sprugel 1985), or the relative proportions of seral stages on a landscape (e.g., Romme 1982; Baker 1989a, c). There are fundamental differences in considering species composition vs. structural attributes such as biomass, age classes, and seral stages. Seral stages or age classes do not become extinct because they can be regenerated by disturbances, provided the species comprising each stage do not become extinct.

Equilibrium in the sense of *absolute constancy*, where there are no changes through time, is the simplest concept that might be applied to a landscape. However, disturbance and change are ubiquitous in ecological systems as disturbances reset succession back to earlier stages, and any concept of landscape equilibrium therefore must incorporate disturbance. Even in the absence of absolute constancy, there may be a particular aspect of a landscape that is invariant. In the *shifting mosaic steady-state* concept (Bormann and Likens 1979), the vegetation present at individual points on the landscape changes, but the proportion of the landscape in each seral stage is relatively constant, i.e., is in equilibrium when considered over a large area or long time period (Fig. 6.19). Bormann and Likens (1979) suggested that, prior to settlement in northern hardwood forests of New England, the standing crop biomass of a watershed or other landscape unit varied slightly around a mean, although the biomass present at any small plot within the watershed fluctuated through time due to treefalls and subsequent regrowth. The shifting mosaic steady-state concept has been difficult to test empirically, but it has been suggested to apply to other systems, such as wave-generated fir forests in the northeastern United States (Sprugel 1976; Sprugel and Bormann 1981) or the fire-created mosaic in the boreal forest in northern Sweden (Zackrisson 1977). The concept applies best

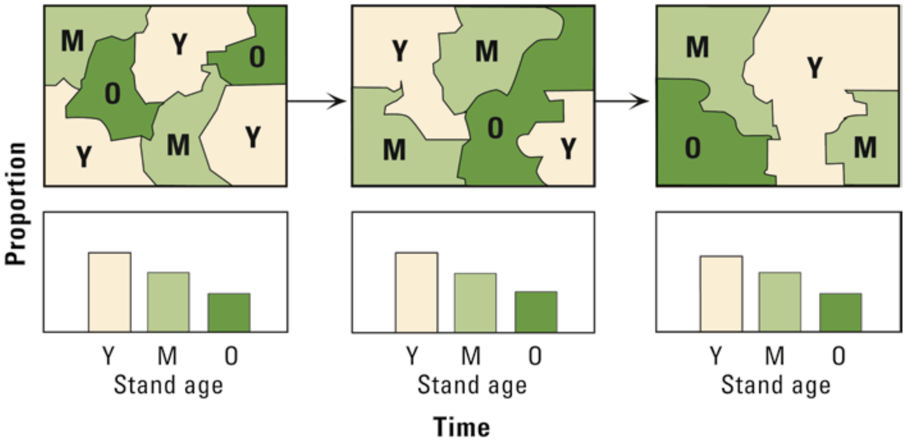

FIGURE 6.19.
Illustration of the shifting-mosaic steady-state concept. *Upper panels* show a landscape at different times in which the shadings indicate different stand ages (*Y* young, *M* mature, *O* old) and their locations through time. The *lower panels* depict the proportion of the landscape occupied by each age class, which remain constant through time. The shifts occur in response to disturbance and succession.

ADAPTED FROM LERTZMAN AND FALL (1998)

when disturbances are small and frequent in a large area of homogeneous habitat (Pickett and White 1985). Shugart and West (1981) suggested that a quasi-steady-state landscape was likely only where the landscape was at least 50 times the average size of disturbances, although Baker (1989a) failed to find equilibrium in the BWCA even at a scale 87 times the mean disturbance-patch size.

Another concept considers landscape equilibrium to be a *stationary process* (i.e., a stochastic process that does not change in distribution over time or space) with episodic perturbation (Loucks 1970). Loucks (1970) suggested that communities may appear unstable at any particular point in time because community composition is changing, but that the entire long-term sequence of changes constitutes a stable system because the same sequence recurs after every disturbance. In fire-dominated landscapes, for example, the statistical distribution of seral stages, time intervals between successive fires, or similar parameters can be determined (e.g., Van Wagner 1978; Johnson 1979; Yarie 1981; Johnson and Van Wagner 1985; Johnson and Gutsell 1994). This concept explicitly acknowledges the stochastic nature of disturbance, but assumes that the distribution of disturbance intervals and the proportion of the landscape occupied by different seral stages remain more or less constant through time. However, the distribution of intervals between disturbances may not be the same, and the probability of disturbance may change with time since last disturbance (Clark 1989).

A concept related to the stationary process is that of *stochastic or relative constancy* through time. Botkin and Sobel (1975) suggested that a system that changes but remains within bounds is a stochastic analogue of equilibrium that is applicable to ecological systems. Harrison (1979) suggested that this concept of a system remaining within acceptable ranges in spite of environmental uncertainty was most relevant to ecology. The idea is akin to the HRV concept, with the dynamics of a response variable in the system remaining between some upper and lower historical bounds. As noted above, this concept is scale-dependent, and long-term directional changes in environmental drivers (e.g., climate) would eventually move a landscape out of its bounds.

The shifting-mosaic steady-state concept provided considerable impetus for studies of landscape dynamics in disturbance-prone landscapes. Romme (1982) studied a 7300-ha watershed on the subalpine plateau in Yellowstone National Park affected by a natural crown-fire regime. He used fire history methods to date fires, age forest patches, and reconstruct that landscape over a 200-year period. He found wide fluctuations in landscape composition and diversity during that time and failed to find any evidence for the existence of a steady-state mosaic (Fig. 6.20). The cycle of extensive fires occurring at intervals of approximately 300 years suggested a landscape characterized by continual change (Romme 1982; Romme and Knight 1982). Romme concluded that this landscape is more appropriately viewed as a nonsteady-state system characterized by cyclic, long-term changes in structure and function. Romme and Despain (1989) expanded this study to an area of 129,600 ha, but still found constant fluctuation in the patch mosaic during the past 250 years. Similarly, Baker (1989a, c) tested for a stable patch mosaic in the 404,000-ha fire-influenced

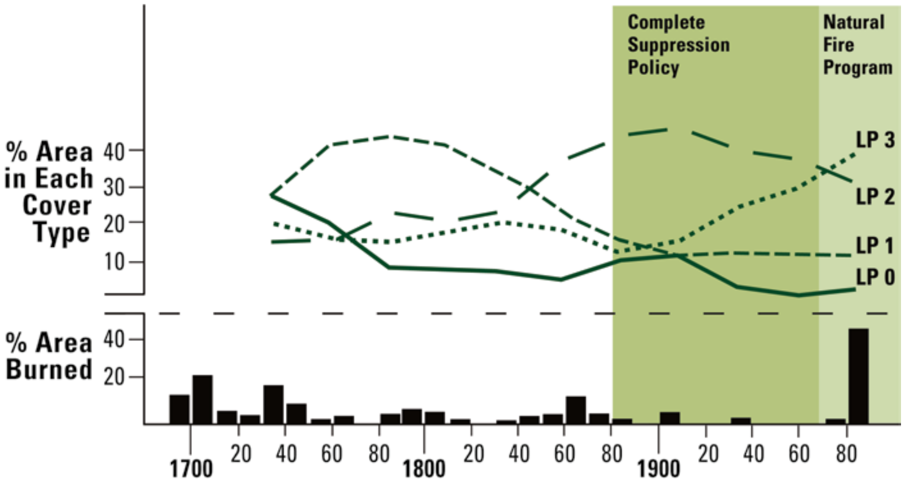

FIGURE 6.20.

(*Bottom*) Percent of a 129,600-ha study area within Yellowstone National Park burned by stand-replacing fires in each decade from 1690 to 1988. (*Top*) Percent of the study area covered by each successional stage from 1735 to 1985. Note the wide fluctuations through time. *LP0* is earliest successional stage in the lodgepole pine forests, extending to about 40 years postfire, *LP1* extends from approximately 40–150 years, *LP2* from ~150 to 250 years, *LP3* >250 years.

ADAPTED FROM ROMME AND DESPAIN (1989)

BWCA, but did not find a stable patch mosaic at any of five spatial scales. He suggested that the lack of a steady-state mosaic was due to (1) spatial heterogeneity in the fire regime, whereby ignition sources, drought severity, fuel load, and fire spread probability, would vary across the landscape, and (2) differences in the scales of fire patches and environmental heterogeneity. Baker (1989a) concluded that the BWCA landscape was a "mosaic of different nonsteady-state mosaics." Indeed, crown-fire-dominated systems may generally be considered as nonequilibrium landscapes (Turner and Romme 1994; Boychuk et al. 1997).

Turner et al. (1993) developed a simple spatial model of landscape dynamics that considered the spatial-temporal scales of disturbance and the resultant landscape dynamics and which could be applied across a range of scales. The model incorporated four major factors characterizing landscape dynamics: disturbance frequency, recovery time, spatial extent of disturbance events, and size of the landscape of interest. These four factors were reduced to two key parameters representing ratios of time and space. The use of ratios in both parameters permits comparison of landscapes across a range of spatial and temporal scales.

The temporal parameter (*T*) was defined by the ratio of the disturbance interval (i.e., the time between successive disturbances) to the recovery time (i.e., the time required for a disturbed site to achieve recovery to a "mature" stage). Defining the temporal parameter as a ratio permitted three qualitatively different states to be considered, regardless of the type or time scale of the disturbance. These states were: (1) the disturbance interval is longer than the recovery time ($T > 1$), so the system can recover before being disturbed again; (2) the disturbance interval and recovery time are equal ($T = 1$); and (3) the disturbance interval is shorter than the recovery time ($T < 1$), so the system is disturbed again before it fully recovers.

The spatial parameter (S) was defined similarly by a ratio of the size of the disturbance to the size of the landscape of interest. Two qualitatively different states were of importance, again regardless of the type of disturbance. These states were (1) disturbances that are large relative to the size of the landscape, and (2) disturbances that are small relative to the extent of the landscape. As defined by Turner et al. (1993), the parameter S could range from 0 to 1; i.e., disturbance events larger than the size of the landscape were not considered. A state space was then constructed with T on the ordinate and S on the abscissa.

A wide range of simulations of disturbance and recovery were conducted, and results tabulated by tracking the proportion (p) of the simulated landscape occupied by different successional changes through time and its standard deviation (Turner et al. 1993). Landscape equilibrium was observed under conditions of small disturbance size and relatively quick recovery times relative to disturbance frequency (Fig. 6.21). A landscape could also appear relatively stable, exhibiting low variance in p values, if increases in disturbance size were offset by decreases in frequency. These conditions resulted in a stable system with low variance in which much of the landscape was still occupied by mature vegetation; this region of the state space may be comparable to the stochastic or relative constancy defined by Botkin and Sobel (1975). The landscape could also appear stable with low variance

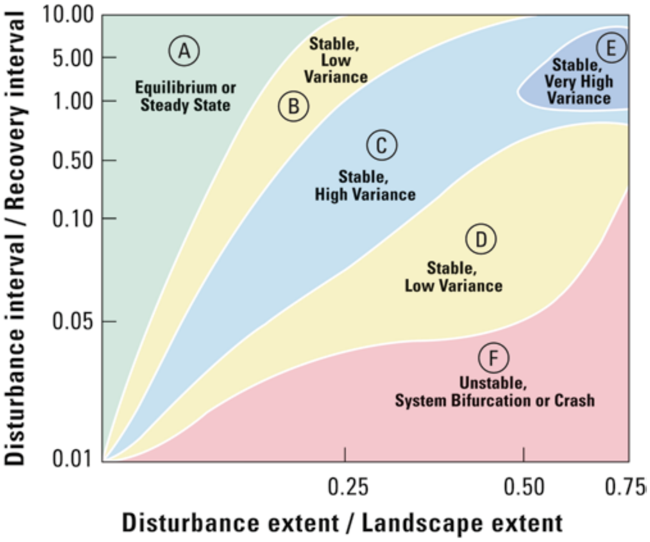

FIGURE 6.21. State-space diagram of the temporal and spatial parameters which illustrates regions that display qualitatively different landscape dynamics. REDRAWN FROM TURNER ET AL. (1993)

when disturbance sizes increase even further, although the early seral stages would then dominate. The landscape may be stable (sensu Loucks 1970) but show very high variance with intermediate values of *S* and *T*, and show extremely high variance when disturbance size exceeds 50 % of the landscape and the disturbance interval is very long. Landscapes in this region of the state space would likely be characterized as nonequilibrium systems.

This model was extremely simple and certainly ignored the biological complexity that would characterize disturbance and succession in real landscapes, and many landscapes are affected by multiple disturbances that occur at different spatial and temporal scales and which may interact. Nonetheless, determination of *S* and *T* parameters for several known landscapes supported the general results (Turner et al. 1993; Fraterrigo and Rusak 2008) and clearly demonstrated the strong influence of scale.

SYNTHESIS

Much of the disagreement surrounding equilibrium versus nonequilibrium, and stability versus instability, can be attributed to several factors: the ambiguity in various definitions, different views of spatial heterogeneity and its effects, the lack of explicit specification of scales, and differences in theoretical foundations (Wu and Loucks 1995; Grimm and Wissel 1997; Perry 2002). Landscapes can exhibit a variety of behaviors under different disturbance regimes, and the same landscape may shift among different regions of behavior. Landscapes that traditionally are considered as being in equilibrium are characterized by small and infrequent disturbance and rapid recovery. Stable systems with high variance are characterized by intermediate size and frequency of disturbance and intermediate rates of recovery. Potentially unstable systems are characterized by large and frequent disturbance and slow recovery. In these landscapes, a system crash or bifurcation to a qualitatively different system is possible (Paine et al. 1998; Romme et al. 1998). Conclusions regarding landscape equilibrium are appropriate only for a specified spatial and temporal scale. Failure to recognize this dependence can lead to sharply different interpretations about the same dynamics.

LOOKING AHEAD: INTERACTING DISTURBANCES AND CHANGING DISTURBANCE REGIMES

Ecologists have made tremendous progress in understanding individual types of disturbance, including quantifying disturbance regimes, describing and explaining the landscape patterns they create, and determining how and when those patterns affect succession. However, key questions remain to be answered. Multiple disturbances affect many landscapes, and understanding how disturbances may interact is an important topic of research in contemporary landscape ecology. Interest in disturbance interactions is driven, in part, by concerns that multiple disturbances could elicit nonlinear responses and unexpected feedbacks, perhaps leading to fundamental system change. Whether global warming will change disturbance regimes and fundamentally alter future landscapes is a related and very important question. Climate change will alter disturbance regimes because many disturbances have a significant climate forcing. Landscape ecologists have recognized these consequences for a long while, but there is an urgent need for more comprehensive evaluations of scenarios of future disturbance regimes (Turner 2010).

Compound and Linked Disturbances

Different disturbances can and will interact with each other. Despite the rapid increase in understanding of the consequences of individual disturbances, their interactions are poorly understood. One type of interaction occurs when prior disturbance exerts a strong effect on ecosystem response to a subsequent disturbance (e.g., Paine et al. 1998; Davies et al. 2009). Paine et al. (1998) suggested that particular co-occurrences or sequences of different disturbances could produce ecological surprises, or qualitative shifts in system state. This notion of *compound disturbances* describes the occurrence of two disturbances in a short window of time that have synergistic effects, which cannot be predicted by summing the effects of the individual disturbances. For example, fires in quick succession reduced seed availability in a black spruce forest (*Picea mariana*) and changed regeneration pathways (Brown and Johnstone 2012). Recent studies have indicated that sequences of extreme events may produce synergistic responses, and furthermore, the sequence itself (e.g., the order of flood and drought) matters (Miao et al. 2009). Understanding the ecological synergisms among disturbances is basic to future environmental management (Paine et al. 1998).

Whether increased disturbance frequency produces a qualitative change in the state of an ecosystem will depend in part on the state of the system when it is disturbed. The "double whammy" will be pronounced if the system has not yet recovered from the first disturbance when affected by the second (Turner 2010). Sequential fires in the same location could convert a forest to nonforest if the interval between the fires was less than the time required for the trees to be reproductive. The cumulative effects of repeated hurricanes could qualitatively change vegetation characteristics and C balance (Busing et al. 2009). However, there remains a paucity of empirical information about whether and when a disturbance will amplify or attenuate the effects of another (Turner 2010).

Another type of disturbance interaction occurs when one disturbance alters the extent or probability of occurrence of another disturbance (Kulakowski and Veblen 2007; Lynch et al. 2006), termed *linked disturbances* by Simard et al. (2011). The first disturbance may either amplify or dampen the second. For example, the extent and severity of bark beetle outbreaks and wildfire have increased in western North America in recent decades (e.g., Westerling et al. 2006; Meddens et al. 2012). These increases re-ignited interest and debate regarding potential interactions between the outbreaks and fire (e.g., Bebi et al. 2003; Jenkins et al. 2008; Derose and Long 2009). Managers and scientists worried that the vast quantities of dead beetle-killed trees on the landscape could increase the risk of high-severity fire, and that fire-injured trees might, in turn, catalyze subsequent bark beetle epidemics. However, there were few empirical data with which to evaluate these potential consequences rigorously.

Emerging research has shown that beetle outbreaks can substantially change the arrangement, quantity, and composition of forest fuels (e.g., Page and Jenkins 2007a, b; Simard et al. 2011; Schoennagel et al. 2012; Donato et al. 2013). However, the potential influence of bark beetle outbreak on fire occurrence or severity depends on timing. Bark beetle outbreaks kill trees over several years, and tree mortality in the affected stand is not synchronous. Shortly after successful beetle attack, the needles on attacked trees become dry, and changes in foliar chemistry make the needles more flammable (Jolly et al. 2012). These factors could increase the likelihood of severe fire, but this effect could be mitigated because the trees also begin to shed their needles, reducing canopy fuels (Simard et al. 2011). Once the outbreak has subsided, however, the amount of canopy fuel is reduced substantially, and this is expected to reduce the risk of high-severity fire until the fuels are replenished through succession. Significant knowledge gaps remain with respect to this disturbance interaction (Hicke et al. 2012b), and the extent to which the behavior of actual fires differ in beetle-killed stands versus unattacked stands remains to be evaluated empirically (e.g., Jenkins et al. 2012). In a regionwide field study in northern Rocky Mountain forests that burned in 2011 and had experienced recent (2001–2010) beetle outbreak, Harvey et al. (2014) found few measures of fire severity were related to prefire outbreak severity. However, it is clear that landscape ecologists must incorporate interactions and feedbacks that may occur among multiple disturbances into their conceptual frameworks and account for superimposed disturbances when describing disturbance mosaics.

Changes in Climate and Disturbance Regimes

Because disturbances are such a key source of landscape heterogeneity, intentional or unintentional shifts in disturbance regimes are likely to alter landscape pattern. Disturbance regimes are remarkably sensitive to changes in key drivers (Fig. 6.3); for example, past climatic changes of small magnitude have caused significant changes in fire regimes in forested landscapes (Green 1982; Hemstrom and Franklin 1982; Clark 1988, 1990; Campbell and McAndrews 1993). Similarly, fire suppression during the past century has lengthened the fire return interval and altered successional pathways in many regions (e.g., Glitzenstein et al. 1995; Linder et al. 1997). In European forests, intensification of disturbance regimes (wind, bark beetle outbreaks, and fire) from 1958 to 2001 was attributed to climate change plus changes in forest extent, structure and composition; disturbance severity was greatest when conducive weather conditions and increased forest susceptibility coincided (Seidl et al. 2011a). Future trends in disturbance size, frequency, and severity are difficult to predict, and changes in disturbance will vary among regions (Hassim and Walsh 2008; Dankers and Feyen 2009; Flannigan et al. 2009; Vecchi et al. 2008). Enhancing our quantitative understanding and ability to predict effects of changing disturbance regimes on landscape structure is a current topic of active research (Turner 2010).

Climate change is expected to strongly influence disturbance regimes because many disturbance regimes have a strong climate forcing. However, key questions remain to be answered. What magnitude of climate change will alter different disturbance regimes? How much do disturbance regimes need to shift before landscape patterns are altered qualitatively? Answering these questions assumes increasing importance in the context of global change. Not surprisingly, changing fire regimes have received considerable attention (e.g., Flannigan et al. 2009; Johnstone et al. 2010; Wotton et al. 2010). In the western United States, the frequency of large fires has already increased in association with earlier spring snowmelt, warmer spring and summer temperatures, and longer fire seasons (Westerling et al. 2006). In portions of the Rocky Mountains, novel fire regimes that are well outside the historical and even paleoecological range of variability are predicted during the twenty-first century (e.g., Westerling et al. 2011). For example, Greater Yellowstone is projected to become much hotter and drier with ongoing climate change, possibly enough to produce substantially different fire regimes (Westerling et al. 2011). Large fires (>200 ha) are anticipated to occur much more frequently than in the past 5000–10,000 years. Years without large fires are expected to become rare with continued warming, and fire rotation is projected to shorten to <30 years from the historical 100–300 years (Westerling et al. 2011). Continued warming could completely transform fire regimes in Greater Yellowstone by the mid-twenty-first century, with profound consequences for patterns and processes. However, how, when, and where such changes might be manifest on the landscape remain to be explored. Once again, variability per se may be very important. For example, the mean annual number of tornadoes has not changed significantly since the 1970s, but variability in their occurrence has increased (Brooks et al. 2014). The number of days per year with tornadoes has declined, but the number of days per year with many tornadoes has increased, but whether this is related to climate change is not yet known (Brooks et al. 2014).

As climate conditions change gradually, disturbance can be the catalyst that triggers rapid ecosystem response to the slowly changing driver. Inertia in ecological communities may mask impending state change because long-lived organisms (e.g., trees) may make the system appear unresponsive to environmental changes even though the regeneration niche may be shifting (Johnstone et al. 2009). Retrospective studies have shown that, in a changing climate, the plant communities that become established following disturbance may differ from those present at the time of the disturbance. On Mt. Rainier, for example, Dunwiddie (1986) demonstrated that fires that occurred during the mid-1800s burned through an *Abies amabilis* and *Tsuga mertensiana* forest that had persisted for centuries. The mid-1800s were characterized by warming temperatures that caused earlier seasonal snowmelt and longer growing seasons. These climatic conditions allowed *Tsuga heterophylla* to become abundant briefly after the fires, and *T. heterophylla* was then replaced by *Abies lasiocarpa*. Because long-lived mature trees may survive short-term climatic fluctuations, species that are best adapted to the current climate may only be able to enter the forest in open habitats following severe fires, and forest composition may respond to climatic changes primarily after disturbance (Dunwiddie 1986). A study by Cwynar (1987) also suggests that, although the ultimate cause of postglacial vegetation change in the Pacific Northwest was climate change, the proximate cause of some postglacial vegetation changes was an altered fire regime.

Rapid post-disturbance ecosystem changes are not just interesting historical stories; rather, they portend changes that are already underway in contemporary landscapes. In the Yukon, Canada, lodgepole pine is extending its range northward following fire, colonizing burned sites previously dominated by spruce (Johnstone and Chapin 2003). In Alaska, white spruce (*Picea glauca*) is replacing black spruce (*Picea mariana*) following fire and permafrost decline (Wirth et al. 2008). In the southern boreal forest of North America, severe windthrow and fire are resulting in rapid shifts in dominant tree species (Frelich and Reich 2010). Forest harvesting may also trigger shifts; aspen (*Populus tremuloides*) has moved to cooler, higher elevations following harvest (Landhäusser et al. 2010). Disturbance may accelerate changes in species composition or even biome boundaries (Frelich and Reich 2010), and potentially hasten transitions to "no-analogue communities" (Williams and Jackson 2007). Such changes have enormous implications for the quantity, quality, and distribution of habitat and will influence the biogeography of many species. If major changes in biotic communities occur after disturbances, there may also be significant consequences for ecosystem processes. Understanding the sensitivity of disturbance regimes to environmental change and the landscape-level consequences of changing disturbance regimes will remain key goals in landscape ecology for the foreseeable future.

SUMMARY

Disturbance creates patterns and is an integral part of many landscapes. The causes, patterns, dynamics, and consequences of disturbances are major research topics in landscape ecology. Disturbance and disturbance regimes are characterized by a variety of attributes, including size, frequency, intensity, severity, and shape. The definition of disturbance is scale dependent.

Are various spatial locations in the landscape differentially susceptible to disturbance? If so, can we predict which areas are more or less susceptible to particular types of disturbance? Results from many studies suggest that landscape position influences susceptibility to disturbance when the disturbance has a distinct directionality such that some locations are usually exposed more than others. In addition, landscape position may influence susceptibility if the disturbance is of moderate intensity, such that its spread is influenced by subtle differences in the landscape. However, if the disturbance itself has no spatial directionality or is sufficiently intense that its spread is unaffected by differences in the landscape, then landscape position does not influence susceptibility to the disturbance.

Understanding how landscape heterogeneity can influence the spatial spread of disturbance has long been a focus of landscape ecological research. Research from theoretical and empirical studies suggests that we cannot generalize to whether landscape pattern always enhances or retards disturbance spread, but its potential effects on disturbance spread may be substantial. If the disturbance spreads within the same cover type, then greater landscape heterogeneity may retard the spread of disturbance. If the disturbance spreads between cover types or is otherwise enhanced by edge effects, then increased greater landscape heterogeneity should enhance the spread of the disturbance. There also may be thresholds in environmental conditions beyond which landscape pattern will not affect the spread of a disturbance.

Landscape epidemiology is an emerging discipline that focuses on the spatial aspects of disease occurrence and spread and overlaps conceptually with landscape disturbance dynamics. Landscape epidemiology studies have revealed effects of landscape pattern on the incidence of many different pests and diseases. Ongoing studies will reveal which local factors and landscape patterns affect susceptibility to a wide range of plant, animal, and human diseases.

Disturbances create very complex heterogeneous patterns across the landscape because the disturbance may affect some areas but not others, and severity of the disturbance often varies considerably within the affected area. These resulting mosaics may show considerable persistence through time.

Disturbance and succession are inextricably linked when we consider landscape dynamics. A thorough understanding of succession must include understanding of how successional processes vary with respect to disturbance intensity, size, and frequency. The availability of propagules is a fundamental determinant of successional patterns and one that can be especially sensitive to the combination of high intensity and large size. If dispersal from outside the disturbed area is important, then the size, shape, and configuration of disturbed patches will influence propagule availability and thus vegetation composition. Spatial effects of disturbance (disturbance size, shape, and arrangement) become increasingly important when residuals are few or sparse and the disturbance is large; under these conditions, colonization, and hence succession, become slower and more difficult to predict.

Applying the theoretical and empirical advances in understanding of how disturbance and succession interact to large, heterogeneous landscapes is challenging because of the spatial interactions and the long time scales involved. Integrated models of disturbance and succession can reveal trends and dynamics in landscapes that cannot be easily observed empirically, and such models may be particularly useful for addressing questions of broad-scale disturbances or global change. Disturbance-succession dynamics are key components of understanding the historical range of variation in landscapes. Landscapes can exhibit a variety of behaviors under different disturbance regimes, and the same landscape may shift among different regions of behavior. Landscapes that traditionally are considered as being in equilibrium are characterized by small and infrequent disturbance and rapid recovery. Conclusions regarding landscape equilibrium are appropriate only for a specified spatial and temporal scale. Failure to recognize this dependence can lead to sharply different interpretations about the same dynamics.

Ecologists have made tremendous progress in understanding individual types of disturbance. Multiple disturbances affect many landscapes, and understanding how disturbances may interact is an important topic of research in contemporary landscape ecology. In addition, because disturbances are a key source of landscape pattern, changing disturbance regimes are likely to alter landscapes. Understanding the sensitivity of disturbance regimes to environmental change, especially climate change, and the landscape-level consequences of changing disturbance regimes will remain key goals in landscape ecology for the foreseeable future.

DISCUSSION QUESTIONS

1. How can a disturbance both create landscape pattern and respond to landscape pattern? Use at least one example of a natural disturbance (preferably, one not discussed in depth in this chapter) to illustrate your answer.
2. Succession is generally defined as change in vegetation through time; thus, temporal dynamics are explicit. Is succession also spatial? Why or why not? Under what conditions will the spatial pattern of disturbance influence succession, and when might such patterns be unimportant?

3. How would you compare a natural and human-driven disturbance regime? What criteria would you suggest for determining whether a human-driven disturbance is comparable to a natural disturbance for a given landscape?
4. Explain how scale dependence is important in understanding disturbance dynamics and the effects of disturbances on a landscape. Consider both spatial and temporal scale.
5. You are charged with developing a strategy for monitoring the effects of disturbance on landscape structure for a large region over the coming century. What would you measure and why? How could you determine the sensitivity of your indicators to changes in the disturbance regime?
6. Are disturbance-driven landscapes stable? Define what you mean by stable, and justify your answer.

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CHAPTER

7

ORGANISMS AND LANDSCAPE PATTERN

Organisms live in heterogeneous environments; they grow, reproduce, disperse, and die in landscapes that are spatially variable and temporally dynamic. Understanding the interactions of organisms with their environment is, of course, a major focus of ecology; understanding the interactions of organisms with the spatial heterogeneity in their environment is a key emphasis of landscape ecology. Much research relating organisms to landscape pattern was motivated by issues associated with *habitat loss* and *fragmentation*. In many landscapes worldwide, expanding human land use has caused natural habitats to decline, and remaining habitat often has been apportioned into small, isolated patches (Fig. 7.1). Landscape ecologists have mounted field studies, developed simulation models, and conducted experiments to understand and predict the consequences of habitat fragmentation for a wide variety of organisms (e.g., Debinski and Holt 2000; Fahrig 2003; Lindenmayer 2006; Collinge 2009). To maintain *biodiversity* (the abundance, variety, and genetic constitution of native animals and plants), ecologists also recognized the need for a landscape perspective to complement population, community, and ecosystem considerations (Franklin 1993). It is not only the local habitat amount and quality that matters for organisms, but also the composition and configuration of the surrounding landscape. John Wiens laid out many of

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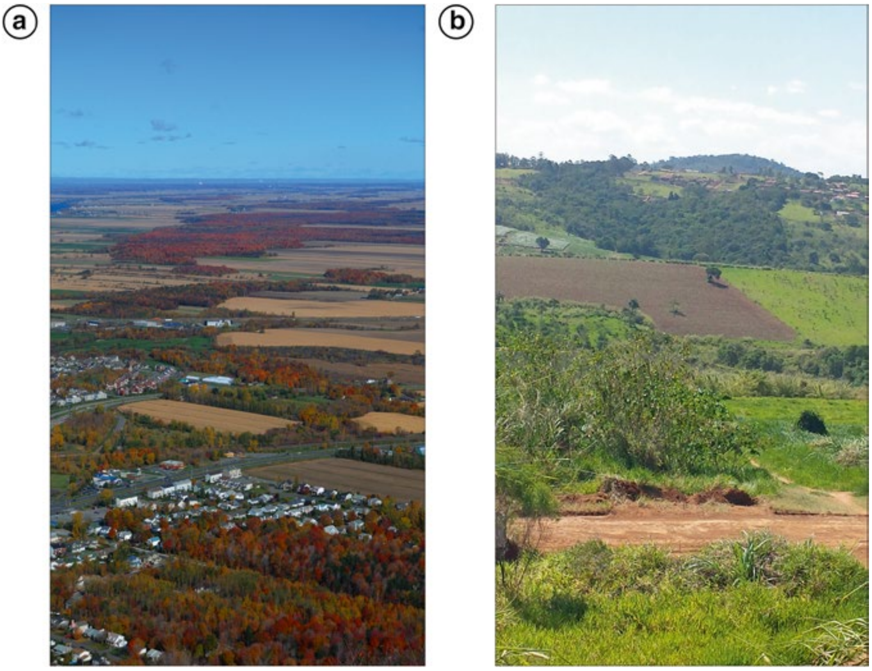


FIGURE 7.1.
(**a**) Fragmented forest in a matrix of agriculture in the Montérégie, Quebec, Canada. Photo credit: Mont Saint-Hilaire Nature Centre. (**b**) Tropical forest fragments are surrounded by clearings and mixed land uses in Brazil.

PHOTO BY ERICA A. H. SMITHWICK

these considerations in 1976 in a seminal review article, "Population dynamics in patchy environments," which still makes for excellent reading. In the introduction, Wiens wrote:

> In the real world, environments are patchy. Factors influencing the proximate physiological or behavioral state or the ultimate fitness of individuals exhibit discontinuities on many scales in time and space. The patterns of these discontinuities produce an environmental patchwork which exerts powerful influences on the distributions of organisms, their interactions, and their adaptations.—(Wiens 1976:81)

Interest in understanding interactions between organisms and spatial heterogeneity is shared among several disciplines, including population ecology, landscape ecology, wildlife ecology, and conservation biology. Spatial structure is now considered an essential element of theories for processes involving genes, individuals, populations, and communities (Kareiva 1990, 1994; Wiens et al. 1993; Hanski and

Simberloff 1997; Zipkin et al. 2009; Lange et al. 2012). Even so, a synthesis among these related fields has yet to emerge. Conventional methods differ among subdisciplines, leading to different emphases on process–pattern dependencies (see Ives et al. 1998). For instance, research in population ecology typically addressed how interactions within and among populations (e.g., competition and predation) generated spatial patterns, which in turn could influence the outcomes of subsequent population interactions. Unlike landscape ecologists, population ecologists did not usually begin with a map describing spatially explicit patterns of resources, and more frequently employed more theoretical and analytical models that were not directly oriented toward a particular organism or management issue (Ives et al. 1998). In contrast, landscape ecologists typically addressed effects of habitat abundance and spatial configuration on a particular population and began with an explicit map of habitat, which might also change through time. Relatively complex simulation models of organisms acting on real (or realistically complex) maps were more frequently used in landscape ecology (e.g., Turner et al. 1995), but landscape ecology was not the only discipline to focus on these issues. A patch-based view of habitat derived from the highly influential theory of island biogeography (MacArthur and Wilson 1967; Haila 2002) became pervasive in landscape ecology. Conservation biology merged approaches from population ecology and landscape ecology to assess habitat and status of threatened or endangered species whose long-term persistence was in jeopardy. Consequently, there is a vast literature and much common ground in the numerous subdisciplines that consider how organisms interact with spatial heterogeneity in their environment.

Recent decades have seen tremendous growth in knowledge relating organisms to landscape pattern and significant expansion of research into many new and exciting directions. Studies have shed light on how landscape heterogeneity affects animal behavior, habitat selection, and movement rates and trajectories; how species interact with one another (e.g., predator–prey dynamics) in complex landscapes; and the patterns and rate of spread of nonnative invasive species. Research has also delved into how the genetic structure of populations varies with landscape structure, and landscape genetic studies have even traced species' migration routes over millennial time scales (e.g., Holderegger and Wagner 2008). Landscape ecologists are also focusing on how changing climate and land-use patterns will affect populations (e.g., Iverson et al. 2011). These topics were barely mentioned in the first edition of this book, but these exciting research avenues have provided important new understanding of organisms and landscapes. We begin this chapter with a brief history of conceptual developments, focusing especially on the paradigm shift from island biogeography to metapopulation biology, expanded views of "habitat" and behavior, and the influence of scale. We next discuss organisms as a cause of landscape pattern, review general understanding of organism responses to landscape pattern, then introduce species interactions, landscape ecology of invasions, and landscape genetics.

CONCEPTUAL DEVELOPMENT OF ORGANISM–SPACE INTERACTIONS

Ecologists have long observed that habitat can be isolated in patches, like "islands" in an inhospitable "ocean" of other land uses. David Lack (1942), for example, noted that remote British islands had fewer bird species than nearer islands. A. S. Watt (1947) pointed out that the isolated patches of vegetation on the heterogeneous landscape were fundamental to understanding community structure. Andrewartha and Birch (1954) discussed the importance of spatial relationships among largely isolated local populations, noting that local extinction of populations was a common phenomenon and that these sites may subsequently become reoccupied. Huffaker (1958) demonstrated how spatial pattern could create stable or unstable dynamics in a predator–prey system. Some of the earliest theoretical work on spatial of dispersal of organisms made analogies to physical diffusion (Skellam 1951). The *diffusion model*, first applied to biological systems by population geneticists (e.g., Fisher 1937; Dobzhansky and Wright 1947), was clearly presented by Andow et al. (1990) and Holmes et al. (1994). Texts by Okubo (1980) and Turchin (1998) also provide a comprehensive discussion of the theory, application, and measurement of diffusion. The basic equation for diffusion of a population of size N is given by:

$$\frac{\partial N}{\partial t} = f\left(N\right) + D\nabla^2 N \qquad (7.1)$$

This equation states that the change in number, N, with time, t, can be estimated by two functions: the description of local population growth $f(N)$, and the diffusion of organisms from the surrounding region. The description of population growth $f(N)$ is dependent on the biology of the organism and the objectives of the investigator, and might be as simple as a linear function of net population growth (i.e., birth minus death) or a complex nonlinear function that can account for density-dependent or competitive effects on growth. The diffusion coefficient D describes how rapidly the population moves in space, and ∇^2 is the "diffusion operator," which describes the rate of change of N with distance (the density gradient). In spite of its simplicity, Eq. (7.1) has had remarkable success in explaining the rates at which species have invaded new environments (Lewis 1997).

Diffusion theory showed that if organisms invade a uniform landscape, the rate of spread, V, will reach an asymptote equal to:

$$V = \sqrt{4rD} \qquad (7.2)$$

where r is the intrinsic rate of population growth. Andow et al. (1990) tested the adequacy of Eq. (7.2) against observed rates of spread for three different species. The results showed that Eq. (7.2) adequately explained the invasion process of muskrats in Europe and the cabbage white butterfly in North America. In general, Eq. (7.2) can give a good approximation of spread across the landscape, providing the data are gathered at sufficiently broad scales. The complexities of actual landscapes are included as the average value of D and, as long as spatial patterns and environmental conditions affecting population growth remain relatively constant, may provide an adequate description of invasion at landscape scales.

The theory of *island biogeography* (MacArthur and Wilson 1963, 1967; MacArthur 1972) was an important influence on how ecologists think about organisms and spatial pattern, and for some time, it was the prevailing paradigm guiding the design of conservation reserves (Haila 2002). Island biogeography was developed as a general theory to predict the number of species found on oceanic islands. The theory predicts that the number of species on an island will reach an equilibrium that is positively related to island size (larger islands would contain more species) and negatively related to distance from the mainland (fewer species on islands far from the mainland, which is the source of new colonists). The number of species on an island depends on the immigration rate of species to the island and the extinction rate of species from the island. Immigration to the island is assumed to be a linear function of distance, d, and also depends on the size of the mainland "source community." Early field studies provided empirical support for the theory (Simberloff and Wilson 1969, 1970). The basic concept was expanded to include alpine zones (Vuilleumier 1970) which have communities isolated on the tops of mountains much like oceanic islands. The theory was also applied to cave communities (Culver 1970; Vuilleumier 1973) for which the landscape separating the mouths of caves functions very much like an inhospitable ocean.

With growing concern about habitat fragmentation, drawing the analogy between habitat fragments and islands was easy, and island biogeography was embraced readily by ecologists. The theory was applied to the design of nature preserves in terrestrial landscapes, generating a long debate among ecologists about whether a single large preserve would be better than having several smaller preserves spaced such that organisms could move among them. The argument centered on the fact that a single preserve might hold more total species, but it could be wiped out with a single catastrophic event. In contrast, the smaller preserves would each contain fewer species, but some preserves would be likely to survive any particular catastrophic event. If even a single small reserve escaped the catastrophe, it would provide a source for recolonization of the damaged areas (Burkey 1989; Soule and Simberloff 1986).

Island biogeography theory was subjected to a number of criticisms (Carlquist 1974; Gilbert 1980), and many modifications have been suggested. Perhaps the primary criticism has been the assumption of equilibrium (Diamond 1972; Terborgh 1975). An island system would require a very long period of time to reach such an equilibrium number of species (Simpson 1974), perhaps best measured in geologic time units during which climate and many other factors change. In many ecosystems, chronic disturbance (Villa et al. 1992) would also invalidate the assumption, because the next disturbance would occur long before the system reached equilibrium. It also has been pointed out that islands close to the shore will experience very large immigration rates (Brown and Kodric-Brown 1977). Immigration could overwhelm the extinction rate so that effects of island size would not be evident, although some models incorporated size-dependent immigration. In addition, island size and distance become less important as dispersal ability increases (Roff 1974). Despite these (and other) criticisms, island biogeography theory was important in highlighting effects of the size and isolation of natural areas on their effectiveness in meeting conservation objectives; indeed, these factors remain important considerations in conservation planning. There is overwhelming evidence that species richness increases with area, whether on islands or on the mainland. However, metapopulation models emerged in the late 1980s as another way of thinking about fragmented habitats and heterogeneous terrestrial environments in general; some authors have referred to this as a paradigm shift (Hanski 1989; Merriam 1991), but it can also be considered as a switch to questions at finer spatial scales than those considered by island biogeography.

Richard Levins (1969, 1970) observed that all populations have a finite probability of extinction, *m*, which is measurably greater than zero and implies that populations will eventually go extinct. However, if the population exists as a patchwork of subpopulations, and the probability of local extinction remains small, then recolonization from neighboring populations may lead to persistence at broader scales. The interconnected set of subpopulations that function as a larger demographic unit was termed a *metapopulation* by Levins (1969). The concepts and terms used in metapopulation theory (Table 7.1) have been readily incorporated into landscape ecology, in part because metapopulation concepts seem to be an apt description of population dynamics in natural or artificially fragmented landscapes. However, it is notable that the Levins' model of metapopulations is *spatially implicit*; i.e., the process of colonization and extinction of suitable habitat patches is independent of their actual spatial locations. Patches that are large or small, or that are a long distance from neighbors, will all have the same probability of colonization and extinction as sites closer to neighbors. This simple formulation also implies that organisms can easily locate all unoccupied patches no matter how far away they may be or how hostile the intervening landscape matrix. Levins' simple metapopulation model has provided important insights but has been notoriously difficult to apply to actual organisms living in real landscapes. The life-history details of each species that govern reproduction and dispersal and the unique spatial patterns of each landscape cause realized dynamics to diverge significantly from those predicted by Levins' simple three-parameter model. Nevertheless, Levins model provided an important starting point for the development of more complex metapopulation models (e.g., Moilanen and Hanski 1998; Wilcox et al. 2006; Graniero 2007).

Table 7.1.
Definitions and synonyms of terms used in metapopulation studies

Term	Synonyms	Definition
Patch	Habitat patch, habitat island, site, locality	A continuous area of space with all necessary resources for the persistence of a local population and separated by unsuitable habitat from other patches (at any given time, a patch may be occupied or empty)
Local population	Population, subpopulation, deme	Set of individuals that live in the same habitat patch and therefore interact with each other; most naturally applied to "populations" living in such small patches that all individuals practically share a common environment
Metapopulation	Composite, population, assemblage (of populations, when local populations are called subpopulations)	Set of local populations within some larger area, where typically migration from one local population to at least some other patches is possible
Levins metapopulation	Classical metapopulation	Metapopulation structure assumed in the Levins model: a large network of similar small patches, with local dynamics occurring at a much faster time scale than metapopulation dynamics
Source–sink metapopulation	–	Metapopulations in which there are patches in which the population growth rate at low density and in the absence of immigration is negative (sinks) and patches in which the growth rate at low density is positive (source)
Turnover	Colonization-extinction events; dynamics	Extinction of local populations and establishment of new local populations in empty habitat patches by migrants from existing local populations
Patch model	Occupancy model, presence–absence model	A metapopulation model in which local population size is ignored and the number (or fraction) of occupied habitat patches is modeled
Spatially implicit metapopulation model	Island model	Model in which all local populations are equally connected; patch models are spatially implicit models
Spatially explicit metapopulation model	Lattice model, grid model, cellular automata model, stepping-stone model	Model in which migration is distance dependent, often restricted to the nearest habitat patches; the patches are typically identical cells on a regular grid, and only presence or absence of the species in a cell is considered (the model is called a coupled map lattice model if population size in a patch is a continuous variable)

Adapted from Hanski and Simberloff (1997)

Metapopulation theory assumes that all patches are of equal quality across the landscape and therefore that birth and death rates are the same in each patch. Ron Pulliam (1988) proposed the special situation of *source–sink dynamics* in which, in a mosaic of habitats, local populations have unique demographic responses to local variation in habitat characteristics (Fig. 7.2). When demographics (birth and death rates) respond to variation in habitat quality, source–sink dynamics emerge (Dias 1996). *Sources* are habitat areas where local reproductive success is greater than local mortality. Populations in source patches produce an excess of individuals who must disperse from where they were born to settle and breed. In contrast, *sinks* are poor habitats where local mortality exceeds reproductive success. Without a new supply of immigrants from nearby sources, these sink populations would go locally extinct. A key insight from this work was that migration of the surplus organisms from the source to the sink could maintain the populations in an apparent demographic equilibrium. Studies of presence only (and even population density) would not detect the negative effect of poor-quality habitat on the population dynamics. Further, removal of patches that were serving as sources for a larger population could lead to catastrophic decline of the population—so patches are not all equal.

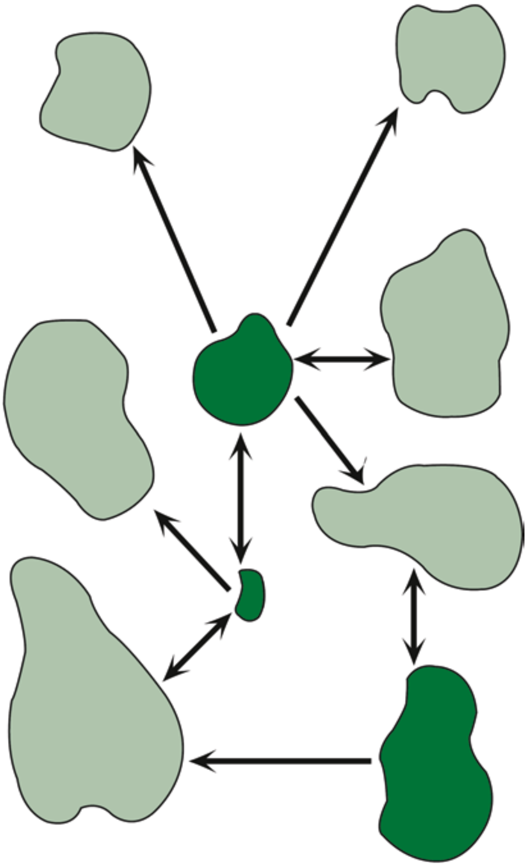


FIGURE 7.2.
Illustration of a metapopulation with source (*dark patches*) and sink (*light patches*) subpopulations. A few source habitats provide excess individuals which then emigrate and colonize sink habitats. *Arrows* indicate the primary directions of movement between patches.

ADAPTED FROM PULLIAM AND DUNNING (1994)

Further, if sink habitat patches are too abundant relative to source habitat patches, the landscape would be unable to support a viable population (Pulliam and Danielson 1991). The maintenance of high-quality habitat on a landscape is important, and the effects of habitat loss cannot be mitigated by the preservation of sink habitat.

There is clearly much common ground between metapopulation biology and landscape ecology, yet Wiens (1997) identified several important differences. Metapopulation models are typically focused on idealized habitat patches in a featureless landscape and emphasize local extinction, interpatch movement, and recolonization. Four features that characterize landscape ecology are largely missing from metapopulation models: (1) variation in patch quality, (2) variation in the quality of the surrounding environment, (3) boundary effects, and (4) how the landscape influences connectivity between patches (Wiens 1997). The interpatch matrix becomes important in landscape ecology because dispersal between patches occurs through the matrix. If the matrix is inhospitable, like the ocean surrounding an island, then isolation becomes more important because the "habitat islands" become isolated from one another (Kennedy et al. 2011). For example, Bolger et al. (1997a) found that the urban matrix was essentially impervious to native rodents in southern California, as animals did not cross even short distances between remnant habitat fragments. If the matrix has relatively low contrast with the habitat patches, complete isolation is much less likely. Metapopulation models also assumed a landscape in which suitable habitat patches occupy only a small proportion of the landscape, whereas landscape ecologists are often concerned with a wide range of proportions of suitable habitat. It is also important to keep in mind that the matrix and the edges of the patches are themselves habitat for other species (McCollin 1993).

What Is Habitat?

A conceptual development in landscape ecology has been a shift toward recognizing habitat as a continuous rather than binary or categorical variable. In a "standard" ecological metapopulation study, an initial task is to distinguish suitable from unsuitable habitat and delimit patches of suitable habitat in a study area (Hanski and Simberloff 1997). Suitable habitat includes areas defined as having the conditions required for a given species to meet its needs for resources, shelter, and successful reproduction. In some instances, the simplifying binary assumption of suitable and unsuitable habitat—sometimes necessary to keep models reasonably simple—is very clear and straightforward. However, in other cases, it can be difficult to partition the landscape into patches of suitable habitat embedded in an unsuitable matrix because habitat quality may vary continuously rather than discretely across the landscape. Thus, landscape ecologists began to expand their view of habitat.

One of the first landscape-level analyses to consider continuous variation in habitat focused on potential habitat for eastern timber wolves (*Canis lupus lycaon*) in the upper midwestern US (Mladenoff et al. 1995). Although driven nearly to extinction during the early part of the century, wolves were gradually expanding their range, moving eastward from Minnesota into northern Wisconsin and the Upper Peninsula of Michigan. Analyses of data from radiocollared wolves revealed that suitable habitat was a function not only of vegetation type and deer density (deer are commonly preyed upon by wolves) but also of land ownership, road density, and human population density across the landscape (Mladenoff et al. 1995). Wolves were moving throughout the landscape and often crossing unsuitable areas. Although successful establishment of a wolf pack was restricted to high-quality habitat, suitable habitat was not simply a binary category but rather a continuous probability surface (Fig. 7.3). While there are areas where the probability of suitable habitat was quite high, there were also extensive areas with moderate probabilities that could provide habitat to sustain wolves.

Another complexity of identifying suitable habitat in a landscape is that a population may require *complementary* or *supplementary resources* from different types

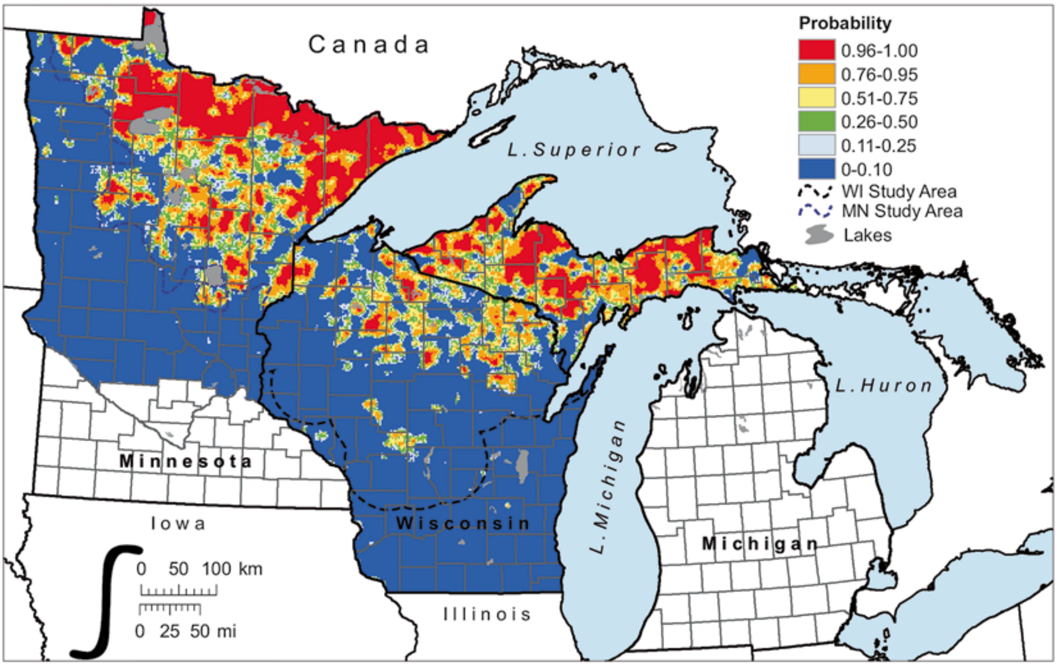


Figure 7.3.

Map of the probability of occurrence of suitable wolf habitat across the upper Midwest, USA, based on spatial extrapolation of a logistic regression model.

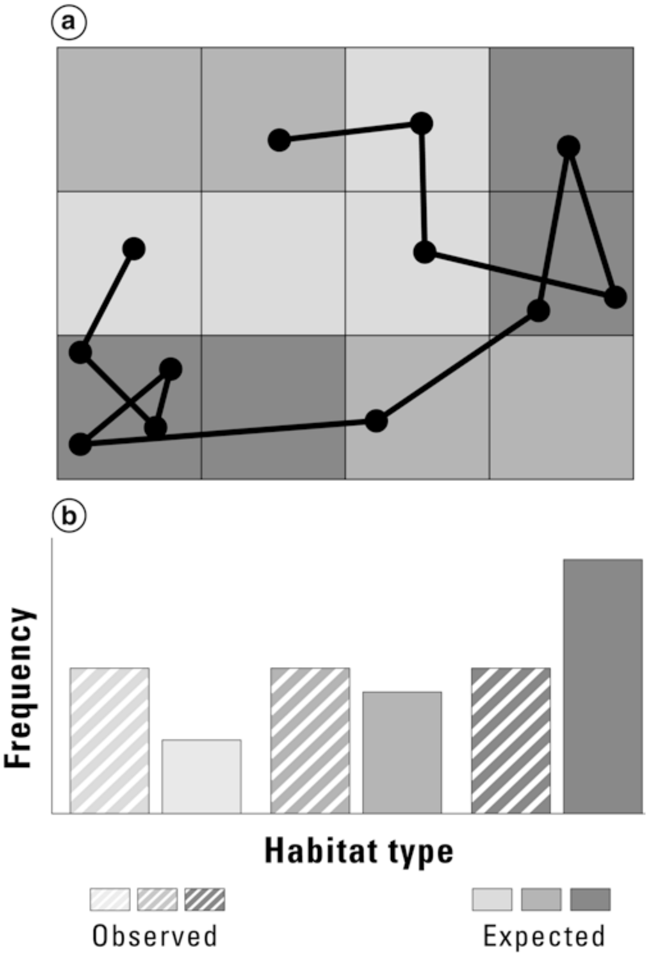
Adapted from Mladenoff et al. (1995)

of habitats or patches (Dunning et al. 1992). Thus, areas of a landscape may need to meet multiple criteria to be considered suitable habitat. For example, wintering birds may use some patches for foraging and others for shelter during storms (Petit 1989). The checkerspot butterfly needs cool slopes for prediapause larvae, but warmer slopes for postdiapause larvae and pupae (Weiss et al. 1988). Barred Owls and Pileated Woodpeckers will supplement their diet from surrounding, suboptimal patches (Whitcomb et al. 1977). In these examples, the populations respond to the spatial patterning of different patches on the landscape, complicating the distinction between suitable and unsuitable habitat. Lastly, landscape ecologists have continued to recognize and demonstrate that habitat definitions will vary among species in a scale-dependent manner (e.g., Wiens 1989; Pearson et al. 1999; Miller and Swihart 2004; Girvetz and Greco 2007). Consequently an organism-centered view of the landscape is required to understand the response of each population to the unique patterns of each landscape.

Landscape ecologists now routinely use sophisticated analyses of habitat use that consider multiple characteristics of the environment and are not based on simplistic patch definitions. *Habitat selection* is the act of choosing the combination of available abiotic and biotic elements that best fulfills the life-history needs of the organism. Habitat selection implies choice among multiple alternatives. What is usually observed is *habitat use*, which refers only to occurrence or presence of an organism at a location and may or may not have been by choice (e.g., a bird might be blown into a habitat by a strong wind rather than having chosen that location). Direct observations (visual or auditory), trapping, and evidence of animal presence (e.g., scat or tracks) provide data on where organisms are found. Advancements in telemetry, such as radio collars or implanted transmitters that provide high-resolution locational data, have catalyzed new studies of how animals use landscapes. Researchers generally document habitat use (i.e., presence or abundance) and infer habitat selection by comparing observed habitat use to available habitat. The gist of these analyses is the expectation that animals will be observed more frequently than expected by chance in their preferred habitats and less frequently than expected in the habitats they choose to avoid (Fig. 7.4). Models that incorporate *resource selection functions* (*RSF*) are commonly used to identify the predictor variables (i.e., resource and habitat conditions) that affect habitat use and the spatial scales of these relationships (Manly et al. 2002; Boyce 2006). Indeed, a value of the RSF approach is the ability to incorporate multiple scales and types of predictor variables, which can include the abundance of other species (e.g., predators or prey) as well as conspecifics (Moorcroft 2012). The RSF models estimate the probability of an organism being present on the landscape, given the characteristics of the site. RSF models can then be extrapolated to the landscape to produce a spatially explicit representation of the probability of space use, which may be considered a continuous rather than categorical map of habitat quality (e.g., Fig. 7.5, Boyce et al. 2003).

FIGURE 7.4.
Schematic illustration of the pathway of an animal as it moves through an idealized heterogeneous landscape with three habitat types that are equally abundant (**a**). The observed and expected frequency of use can be compared (**b**). In the absence of any preference, animals would be expected to use the habitats in proportion to their availability. Here, the actual distribution of locations would indicate that animals preferred the habitat indicated by the *darkest shading*.

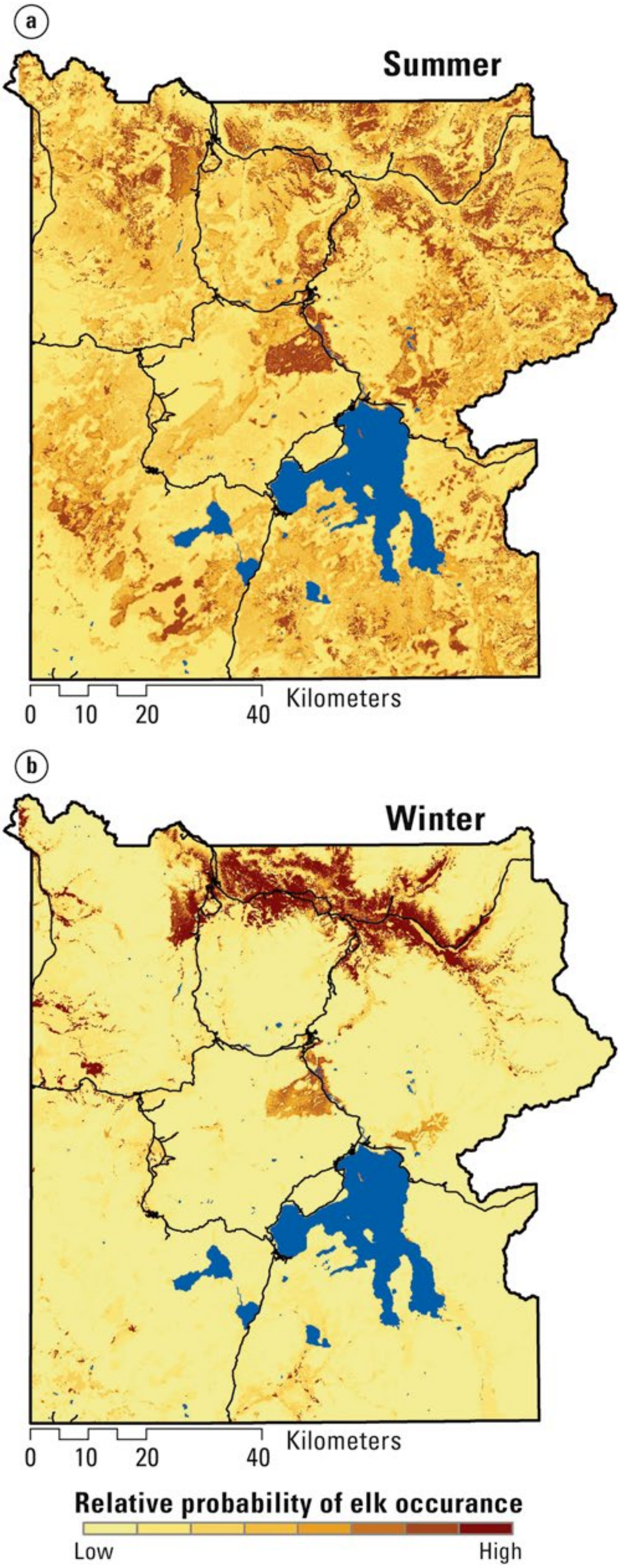
ADAPTED FROM MOORCROFT (2012)



As advances in telemetry facilitated studies of habitat use, they created new opportunities for studying actual movement pathways and understanding fine-scale habitat selection in heterogeneous landscapes. The high sampling frequency of telemetry data made possible by global positioning systems (GPS)-based telemetry systems made it possible to resolve animal spaces use along a path of relocations, leading to step-selection analyses (e.g., Gustafson and Gardner 1996; Morales et al. 2004; Lookingbill et al. 2010). *Step-selection* evaluates habitat selection based on what is available to an individual animal given its current position, rather than in the landscape overall, and on the individual's physiological or behavioral state (Morzillo et al. 2011; Moorcroft 2012). Step selection recognizes that organisms choose where to go next based on what is accessible from where they are, and it is a fine-scale assessment of habitat use and selection.

FIGURE 7.5.
Seasonal maps of the relative probability of elk occurrence in Yellowstone National Park in summer (**a**) and winter (**b**) based on telemetry data and a resource selection function that was extrapolated spatially.

FROM BOYCE ET AL. (2003)



Analysis of movement trajectories and step selection can produce different and complementary insights compared to landscape-level RSF analyses. For example, in a study of elk habitat use in Yellowstone National Park, landscape-level analyses revealed strong habitat selection by elk (Boyce et al. 2003). Fine-scaled analyses of movement trajectories of individual elk were consistent with the landscape analyses, although the importance of different predictors varied among individuals (Forester et al. 2007). However, the movement analyses revealed that landscape-level patterns of movement were driven by animals moving frequently among preferred locations, rather than staying for extended periods of time within preferred habitat (Forester 2005; Forester et al. 2007). This behavior could be part of a predator–prey *shell game* (Mitchell and Lima 2002), in which prey (elk) move purposefully about the landscape to avoid detection by predators (wolves). A key general insight was that landscape patterns of habitat selection could not be used to infer fine-scale habitat use and movement dynamics (Forester et al. 2007). This example also illustrates habitat selection at multiple scales and variation among individuals of the same species.

Behavioral Landscape Ecology

Predicting how animals will respond to climate and land-use change is increasingly important in ecology, and this requires knowledge of how animals behave in real landscapes—how individuals move through a landscape, how they select habitat, and how these choices affect reproductive success (Knowlton and Graham 2010). Movement, dispersal, and habitat selection are well-represented themes in animal ecology, and animal decision-making has been studied by behavioral ecologists for a long time (Lima and Zollner 1996; Moorcroft 2012). However, until recently, there was surprisingly little overlap between behavior and landscape ecology. In their article identifying the need for "a behavioral ecology of ecological landscapes," Lima and Zollner (1996) attributed this divergence to vast differences in the scales of thought and study. The emerging field of *behavioral landscape ecology* bridges this divide to explore how behavior of a particular species responds to landscape heterogeneity and changing landscape patterns (Knowlton and Graham 2010). Behavioral landscape ecology seeks to understand the mechanisms that underpin landscape distributions of animals and to develop methods for predicting how animals will respond to changes in their landscapes. For many animals, the movements of individuals are influenced not only by their current environment but also by the history of their past movements. Thus, the role of memory is also key for understanding animal movement and home ranges (Moorcroft 2012).

Although the integration of behavior and landscape ecology is relatively new, Knowlton and Graham (2010) identified general trade-offs between movement and mortality risk from studies to date, including: (1) movement is usually faster and more directional in unfamiliar or suboptimal habitats, (2) movement appears to be augmented for most taxa when corridors were present, (3) movement patterns depend not only on patch characteristics but also on the surrounding landscape, and

(4) movement behavior differs between habitat generalists and specialists. A variety of different behaviors or traits can be incorporated directly into studies of organisms in heterogeneous landscapes (Table 7.2). Continued research in behavioral landscape ecology promises to improve the ability to anticipate animal responses to changing landscapes and is important for understanding species interactions.

Studies of organism movements in heterogeneous landscapes and the consequences of movement for population dynamics remain challenging. A review of >400 studies of movement among habitat patches found that most studies did not report rates of interpatch movement and even fewer attempted to determine population consequences of these movements (Bowne and Bowers 2004). It is inherently difficult to measure movement, yet population density and even occupancy or habitat selection can be poor substitutes for actual movement. Further, despite the increased availability of GPS-telemetry data, significant challenges in working with these data remain to be addressed (see Hebblewhite and Haydon 2010).

Models complement field studies in behavioral landscape ecology. For example, computer simulation of movement can provide insight into functional connectivity (e.g., Vogt et al. 2008; Lookingbill et al. 2010), which can be depicted using network models that incorporate nodes, links, and components that are individually scaled for each species. New approaches based on social networks (e.g., Fletcher et al. 2012) are helpful for evaluating scale-dependent connectivity patterns based on movement abilities of different species. These analyses are particularly useful for defining attributes of the matrix that either promote or prevent movement (Lookingbill et al. 2010), as well as identifying smaller patches that serve as stepping stones connecting larger areas that may sustain species within the landscape (Vogt et al. 2008; Saura et al. 2011; Hodgson et al. 2012).

Scale Matters

Recognition that species interactions with landscape pattern were scale dependent evolved concurrently with landscape ecology (Wiens 1989). As with landscape level and step selection of habitat, conclusions about how species respond to pattern at one scale are difficult to translate to another species at another scale. Similarly, a resource patch for one species is not necessarily a resource patch for another, which implies that descriptions of patchiness are species and process specific (Fig. 7.6); a beetle does not relate to its environment on the same scales as a vulture, even though both are scavengers. Returning once again to John Wiens (1976) review article, we read:

> First, it is essential that the fabric of spatial scales on which patchiness is expressed be unraveled, and the structure of spatial heterogeneity be related to the variations in environmental states on diverse time scales. The key to achieving this is in shedding our own conceptions of environmental scale and instead concentrating on the perceptions of the organisms, attempting to view environmental structure through their senses.—(Wiens 1976:110)

Table 7.2.
Behavioral measures or traits that can be quantified and are useful in studies or models focused on understanding how organisms use heterogeneous landscapes

Behavior or trait	Definition	Example of usefulness in landscape studies
Perceptual range	Distance at which features (such as habitat elements) can be detected by the species	Can be used to create a buffer, or probability boundary, in which an organism can perceive a particular feature or resource in the surrounding landscape
Homing ability	The species' ability to return to its home range when it is away from its home range	Can help to define maximum dispersal distances and least-cost movement pathways
Habitat or matrix permeability	The probability an individual will move through habitat or matrix; crossing probability is high in areas that are more permeable	Can be used to define resistance or friction level for a landscape and to identify least-cost pathways of movement
Habitat selection	An individual detects differences in habitat or resources and chooses one area over others	Can identify preferences for different patches or areas of the landscape and locations where organisms are most likely to occur
Gap-crossing ability	The species' ability or willingness to traverse areas of matrix vegetation or suboptimal habitat	Can help to define least-cost pathways and dispersal abilities and to set scales that determine relative patch isolation
Corridor use	Ability or willingness of a species to move through a narrow stretch of habitat that connects larger areas of habitat	Helps to define least-cost pathways of movement and dispersal capacity in varying landscapes
Con-hetero-specific attraction/repulsion	Alteration of movement behavior when members or the same species are detected, or as a function of local population density	Population density can change the attractiveness of different habitat patches and may influence reproductive success
Perceived predation risk	An animal's sense of danger from predators; responsiveness to landscape of fear	May change the attractiveness of different habitat types or landscape positions; may have consequences for fitness

Modified from Knowlton and Graham (2010)

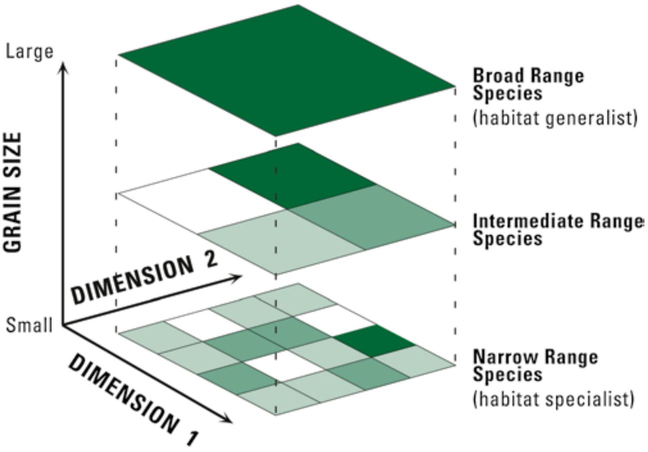


FIGURE 7.6. Conceptual model of habitat structure in which homogeneity and heterogeneity depend upon the species and the resolution at which species perceive their environment.

ADAPTED FROM KOLASA (1989)

There is a strong imperative to focus on the scales that are appropriate for the organism, and to recognize that our human-based perception of scale and pattern may not be the right one. But why do appropriate scales differ among taxa, and how is the "right" scale determined?

Some scale dependencies are due to functional traits, or attributes, of the species, especially those related to mobility or dispersal capability. For example, vagile species may be less sensitive to fine-scale patterns of adjacency than sedentary species or those with limited dispersal distances. In the species-rich mesic forests of the Southern Appalachians, studies of forest herbs have demonstrated that native herbaceous species with good dispersal (e.g., maidenhair fern, *Adiantum pedatum*) are found in small, isolated forest patches, but species with limited dispersal (e.g., the ant-dispersed bellwort, *Uvularia grandiflora*) are absent from small, isolated forest patches (Pearson et al. 1998). Similarly, in a cross-continental synthesis of published studies of how butterflies and moths respond to habitat area and isolation, Ockinger et al. (2010) found that species with low mobility, a narrow feeding niche, and low reproduction were most strongly affected by habitat loss. Body mass may also be important, and strong relationships between body size and habitat-selection scale imply evolutionary adaptation to landscape heterogeneity (Fisher et al. 2011).

To test experimentally for among-species differences in scales of interaction with patch structure, With (1994b) studied three grasshopper species of different body size using "microlandscapes" (Wiens and Milne 1989; Johnson et al. 1992). The study was conducted in grassland habitat, and 25-m^2 microlandscapes were established in which the heterogeneity of shortgrass cover was varied by establishing replicated treatments with different amounts of grass and arrangements of grassy habitat. With (1994) recorded the movement patterns of the grasshopper species in these different landscape mosaics and applied fractal analysis to compare the landscape perceptions of the different species in the same environments. Results demonstrated that the largest of the grasshopper species moved up to six times faster than the two smaller species, and the species responded differently to micro-landscape structure in the 25-m^2 plots. The two smaller species also had more complex movement patterns than the larger species, suggesting that these species were interacting with patch structure at a finer scale of resolution than the larger species (With 1994). She concluded from these studies that the grasshopper species were scaling the landscape differently, and suggested that the scale independence of fractal analysis provides a useful tool for identifying such differences among taxa. Thus, the scale of pattern interacts with the scale at which an organism operates to determine its dynamics on a given landscape, and it follows that connectivity is a scale-dependent phenomenon. Whether habitat is connected or not depends on both habitat abundance and spatial arrangement, as well as the movement or dispersal characteristics of the organism.

It is easy to say that interactions between species and spatial heterogeneity are scale dependent, but it can be very difficult to identify the "right" scales in practice. Without a reasonable means of resolving issues of scale, comparisons across species and landscapes are more likely to be misleading than useful. Even different life stages within a species may operate at different scales on the landscape, especially if the life stages differ in vagility and size [e.g., nymphal (flightless) and adult (flighted) grasshoppers; With 1994]. The concept of *ecological neighborhoods* (Addicott et al. 1987) offered a practical and useful way of identifying scales.

Addicott et al. (1987) proposed that ecological neighborhoods for an organism be empirically defined by using three criteria: (1) a particular ecological process (e.g., foraging, reproduction), (2) a time scale appropriate to the process (e.g., day, week, season, year), and (3) the organism's activity or influence during that time period. By tracking the space the organism uses during the time period and focusing on the process, the spatial extent used can be estimated by applying a criterion, e.g., the 95 % of the activity is included in a particular area (Fig. 7.7). This then is the organism's neighborhood. Note that specifying a particular process is important because the ecological neighborhood of an individual's daily foraging may be quite different from that of its annual reproductive activities. The distribution of patches, their isolation, and their temporal duration can then be assessed relative to the size of the neighborhood by defining the following metrics: (1) rp = relative patch size = patch size (m^2)/neighborhood size (m^2), (2) ri = relative isolation = interpatch distance (m)/neighborhood radius (m), and (3) rd = relative patch duration = patch duration (t)/neighborhood duration (t). By using relative metrics the effect of scale is removed (note that rp, ri, and rd are all dimensionless) and dynamics of different species may be compared. For example, a 10-ha habitat patch for a grizzly bear foraging over a 1000-ha landscape may be functionally similar to a 0.10-habitat patch for a raccoon that forages over a 10-ha area; in both cases, the $rp = 0.01$, even though the resource patches themselves were quite different.

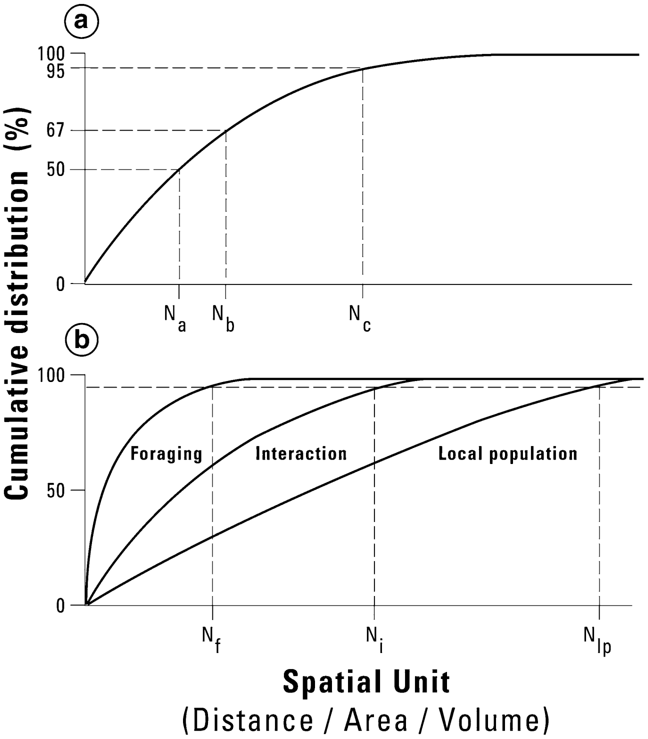


FIGURE 7.7.

Hypothetical examples of the relationship between cumulative distribution of movement or influence against spatial unit as a means of identifying the ecological neighborhood of an organism. (**a**) *Dotted lines* at arbitrary points on the cumulative distribution indicate different neighborhood sizes for different decision criteria. (**b**) Each curve represents a cumulative distribution with an associated neighborhood size for a different ecological process using a decision criterion of 95 %.

MODIFIED FROM ADDICOTT ET AL. (1987)

An organism's perception of heterogeneity clearly depends on its scale of activity, and this approach offers a practical way to identify and compare patchiness across a range of different species.

Given that the scale at which organisms use their environment may differ greatly among species, how do we best determine the optimum scale for relating population responses to the structure of the surrounding landscape? Simulation analyses that incorporated the effects of dispersal distance, reproductive rate, and movement behavior offer some guidance (Jackson and Fahrig 2012). Modeling results indicated that dispersal distance has a strong, positive influence on the scale of effect (i.e., species with longer dispersal distance respond to landscape patterns at larger scales); Jackson and Fahrig (2012) suggest using a radius of 4–9 times the median dispersal distance when assessing population responses to the surrounding landscape.

An added complexity to the problem of identifying appropriate scales is that many organisms respond to heterogeneity at multiple scales rather than at a single scale. A variety of authors (e.g., Addicott et al. 1987; Senft et al. 1987; Wiens 1976, 1989; Kotliar and Wiens 1990; Pearson et al. 1995) suggested that animals make scale-dependent choices in habitat use and/or foraging, and many studies have since documented such relationships. For example, elk in Yellowstone National Park respond to environmental heterogeneity at multiple scales (Pearson et al. 1995; Boyce et al. 2003). A study of Eurasian lynx (*Lynx lynx*) in southern Norway used spatial variation in human disturbance and its consequences for lynx survival to test a hierarchical habitat selection hypothesis (Rettie and Messier 2000) and found strong evidence of scale-specific heterogeneity driving individual spatial behavior (Basille et al. 2013). Patterns of plant occurrences may also reflect heterogeneity at multiple scales. For example, species richness in grassland communities in Estonia was related to scale-dependent factors (Gazol et al. 2012). At the landscape scale, species richness was positively related to historical habitat availability, whereas at fine scales, species richness was related to light heterogeneity, shrub cover, and soil depth heterogeneity (Gazol et al. 2012). The multiple scales at which species perceive or respond to their environment, and the fact that these scales often differ from our own, must be recognized in any attempt to understand or predict the response of organisms to spatial heterogeneity. Because species differ in their scales of resource use, studies of species interactions are particularly sensitive to scale (Wiens 1989). Understanding the organism responses to spatial pattern at multiple scales remains a fundamental component of landscape ecology.

EFFECTS OF ORGANISMS ON LANDSCAPE HETEROGENEITY

The effects of spatial pattern on organisms get the lion's share of attention in landscape ecology, but organisms can also create pattern. Organisms can produce or maintain spatial heterogeneity through physical alteration of the environment and by feeding activities. The concept of organisms as *ecosystem engineers* was proposed by Jones et al. (1994, 1997) to describe organisms that directly or indirectly modulate the availability of resources to other species by causing state changes in biotic or abiotic materials. In so doing, ecosystem engineers modify, maintain, or create habitats. All organisms modify their environment to some extent, but the concept of ecosystem engineering emphasizes physical modifications that are relatively large within the focal landscape (Wright and Jones 2004, 2006). Examples include organisms as diverse as elephants, beavers, bison, deer, trees, and earthworms, all of which physically modify the environment. Despite some differing opinions over semantics (e.g., whether organisms create patterns intentionally or inadvertently), the concept is useful in landscape ecology when thinking about causes of spatial pattern.

A classic example of an ecosystem engineer is the dam-building beaver (*Castor canadensis*), whose influence in structuring landscapes has been well recognized in landscape ecology (Johnston and Naiman 1990a, b; Little et al. 2012). These animals create ponds and wetlands by damming streams, and they initiate secondary succession when dams are abandoned and ponds drain (e.g., Remillard et al. 1987; Johnston et al. 1995). Beaver dams not only retain water, but they also trap large volumes of sediment that would normally erode downstream. These activities create a mosaic of temporally and spatially variable habitat patches, which have profound long-term consequences for the whole drainage network (Naiman et al. 1994). The "beaver meadows" resulting from dam abandonment can persist for over 50 years (Pastor et al. 1999); on Mount Desert Island, Maine (USA), the variation in wetland communities was driven by gradients of time since beaver dams collapsed (Little et al. 2012). Variation in beaver-created habitats has consequences for species diversity. For example, in the central Adirondack Mountains (New York, USA), beaver increased the number of herbaceous plant species in the riparian zone by 33 % by increasing habitat heterogeneity (Wright et al. 2002). By modifying the plant community, other taxa, such as insects, may be indirectly maintained in the landscape by beaver (Bartel et al. 2010), and biogeochemical cycling is also affected (Naiman et al. 1994). Ecosystem engineers will increase species richness at the landscape scale whenever there are species present in a landscape that are restricted to the engineered habitats during at least some stage of their life cycle (Wright et al. 2002).

Other large animals also modify habitat structure and/or function (Naiman and Rogers 1997). Along river corridors in southern Africa, hippopotamus make nightly feeding forays between rivers and surrounding riparian zones and create a maze of trails and canals that provide movement corridors for many other species (Fig. 7.8; Naiman and Rogers 1997). During the daytime, hippopotamus also deepen pools and create habitat for crocodiles and large fishes. In North American grasslands, *Bison bison* create unvegetated patches (wallows) that provide habitat for fugitive species (Knapp et al. 1999). Smaller animals may also be effective engineers. For example, grazing by Lesser Snow Geese (*Chen caerulescens*) and the activities of earthworms (Holdsworth et al. 2007) produce fundamental changes in soil profiles (Johnston et al. 1971; Hedde et al. 2013). From a landscape perspective, organisms can be key causes of altered physical habitat conditions and landscape heterogeneity.

The concept of *foundation species* (Dayton 1972; Ellison et al. 2005) recognized the fundamental role of dominant (abundant) organisms that provide the physical structure for the rest of the community. Foundation species alter the abiotic conditions and provide a resource base and substrate for the other populations in the ecosystem. Often times, a dominant plant species occupies this role. For example,

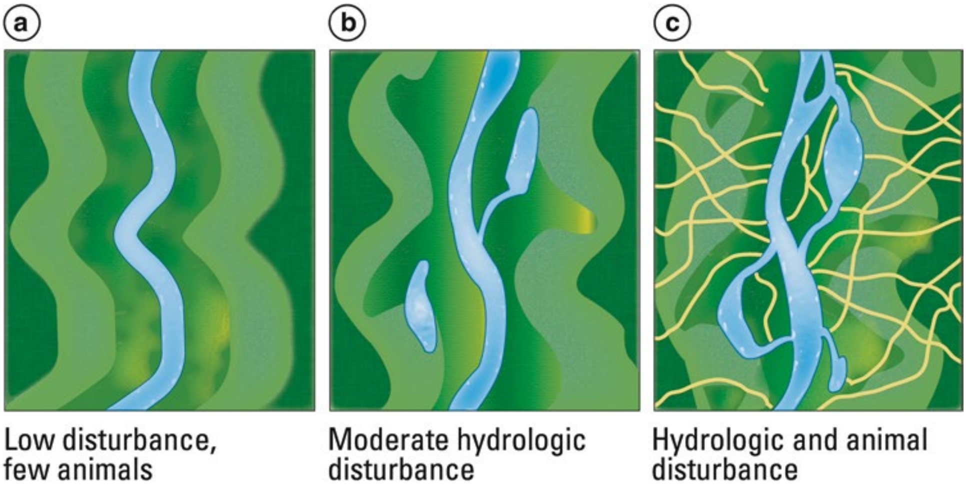


Figure 7.8.
Activities of large animals, such as hippopotamus, act as ecosystem engineers by physically modifying their environment, as shown here for riparian corridors in African rivers.

Modified from Naiman and Rogers (1997)

Douglas-fir (*Pseudotsuga menziesii*) dominates young and old-growth forests in many areas of the Pacific Northwest of North America. The live trees, standing snags, and downed logs provide unique habitats for many other species, including the Northern Spotted Owl (*Strix occidentalis*). In coastal landscapes in the tropics, dense often-monospecific mangrove (*Rhizophora* spp.) forests provide habitat for myriad other species (e.g., Bishop et al. 2012) and play a key functional role with respect to carbon storage (Donato et al. 2011). Multiple foundation species assemblages also can drive landscape-scale patterns of communities and ecosystem function (Angelini et al. 2011).

The loss of foundation species can trigger an unexpected cascade of consequences throughout a landscape (Ellison et al. 2005). In the southern Appalachian Mountains, widespread mortality of eastern hemlock (*Tsuga manadensis*) due to the nonnative hemlock woolly adelgid (*Adelges tsugae*) is changing forest structure (Ford et al. 2012) and prompting land managers to plan for short- and long-term effects of substantial decline in hemlock, the foundation species (Vose et al. 2013). Widespread drought-induced mortality of *Juniperus monosperma* in a northern Arizona woodland resulted in major changes in plant population dynamics and ecosystem function, and increased the presence of cheatgrass (*Bromus tectorum*), a highly invasive graminoid (Kane et al. 2011).

Although this overview of organisms as agents of landscape change and pattern generation is brief, it is important to remember that the interaction between organisms and landscapes is always reciprocal. Some authors are now considering interactions between ecosystem engineers and foundation species, as exemplified by studies of grazing by waterfowl (ecosystem engineers) that affects the distribution of a foundation seagrass (*Zostera noltii*) that increases the spatial complexity of a coastal landscape (van der Heide et al. 2012). However, organism-based studies in landscape ecology to date have primarily focused on how organisms respond to, rather than generate, spatial patterns, making this a rich area for future research.

RESPONSE OF ORGANISMS TO LANDSCAPE HETEROGENEITY

Landscape patterns are continually altered by natural disturbances and human activities, resulting in changes in the relative abundance and spatial arrangement of different habitats and/or changes in habitat quality. There is strong interest in how such changes affect the distribution, abundance, and persistence of species across landscapes. The number and diversity of studies that address this topic is truly overwhelming, and our treatment cannot even attempt to be comprehensive. Rather, we briefly summarize general insights that emerged from landscape ecological studies about organisms and space that are now widely recognized. This section ends with a synthesis, suggesting the conditions for which spatial pattern will be important for organisms.

General Insights, from Patch to Landscape

In general, larger more heterogeneous patches contain more species and often a greater number of individuals than smaller more homogeneous patches of the same habitat. Patch size is an important characteristic of landscape structure. There is overwhelming evidence from many taxa and geographic locations that larger patches support a greater number of species (Joshi et al. 2006; Kappes et al. 2009), and that an increase in within-patch heterogeneity (e.g., vertical complexity, microsite variety) will generally increase species richness. This is not surprising based upon the well-documented relationship between species and area (Huston 1994; He and Legendre 2002), and it occurs for several reasons. The larger the habitat patch, the more local environmental variability is contained within it, such as differences in microclimate, structural variation in plants, and diversity of topographic positions. This variability provides more opportunities for organisms with different requirements and tolerances to find suitable sites within the patch.

The relative abundance of edge and interior habitat affects species diversity within a patch. Patch edges and interiors may have different conditions that favor some species but not others, and the relative abundance of edge versus interior habitats varies with patch size. Smaller patches have a greater perimeter:area ratio than larger patches, which means that smaller patches will have a greater proportion of "edge habitat," and larger patches will have a greater proportion of "interior habitat" (Fletcher et al. 2007). Edge effects can extend to variable distances within a patch depending on the habitat type and the measured response (e.g., temperature, humidity, light, species presences or use). Floristic studies in ancient forests (i.e., forests that have never been cleared for agriculture) in northern France indicate that edge effects can be detected at distances in excess of 500 m (Berges et al. 2013). Related to the effect of patch size on edge habitat is the effect of patch shape on the boundary, or *ecotone*, between two cover types. Simple shapes (like circles) have a lower perimeter:area ratio than do complex shapes of the same area. Human activities often simplify boundary shapes, changing complex patch boundaries that may follow topographic variability or result from natural disturbance into straight lines (Krummel et al. 1987).

A review of theoretical and empirical studies of species interactions with habitat edges (Fagan et al. 1999) suggested four general classes of effects: (1) edges may be barriers or filters to movement, (2) agents which alter mortality rates, (3) areas providing energetic subsidies or refuge, and (4) as regions where novel interspecies interactions may occur. The wide differences in response of different species to edges can result in very different effects. Fagan et al. (1999) noted that knowledge of "edge-mediated dynamics place(s) severe limitations" on our understanding of processes leading to species colonization or extinction, which comprise the conceptual core of island biogeography and species–area relations.

Despite many observations of species richness increasing with patch size, the effect of patch size alone is not easily determined. Patch characteristics may fail to predict species occurrence in a particular patch because the conditions of the surrounding landscape also play an important role. In an analysis of *occupancy* (i.e., presence or occurrence) data from 1015 bird, mammal, reptile, amphibian, and invertebrate populations on six continents, Prugh et al. (2008) found that patch area and isolation were surprisingly poor predictors of occupancy for most species. Their analysis highlighted the importance of characteristics of the intervening or surrounding matrix (Prugh et al. 2008)—which we consider in greater detail.

Characteristics of the surrounding landscape can strongly influence local populations within a patch. The presence or abundance of organisms at a given location or within a particular patch is often explained by characteristics of the focal patch and by *landscape context*, i.e., attributes of the surrounding landscape, although the relative importance of these two levels of influence varies among taxa. An early paper by Jerry Franklin (1993) argued that understanding attributes of the matrix, which allow species to move through landscapes, was essential when designing habitat reserves. One of the first field studies designed to evaluate effects of the landscape matrix on populations was conducted by Scott Pearson (1993), who studied wintering birds in powerline rights-of-way (ROW) in the Georgia piedmont. These ROWs are corridors in which the vegetation is maintained in an open state, usually

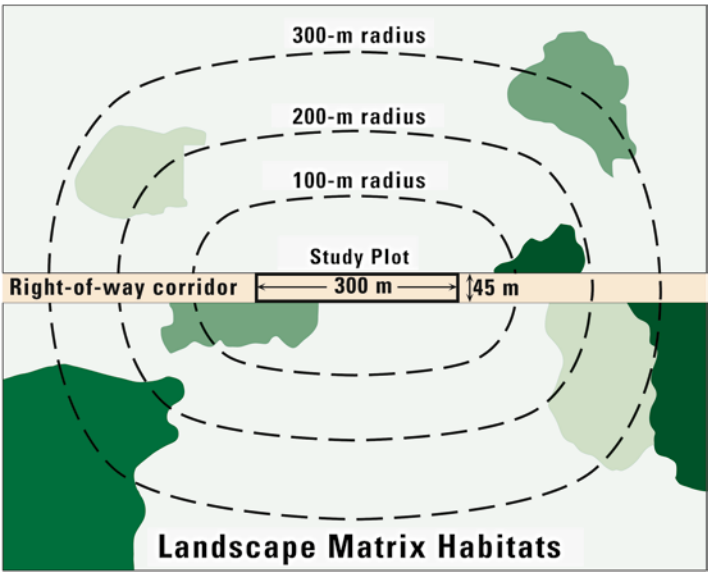


FIGURE 7.9.
Illustration of different spatial extents at which landscape patterns were characterized by Pearson (1993) and used in statistical models of bird species presence and abundance in powerline right-of-way sample plots.

ADAPTED FROM PEARSON (1993)

by mowing, so that shrubs and herbaceous plants dominate. The areas surrounding the ROW may also be open, forested, or in cultivation. Pearson recorded the abundance of different bird species and the characteristics of the vegetation (such as height, density, and species composition) within each ROW, and quantified the types of habitats in the surrounding landscape based on aerial photography (Fig. 7.9). He found that variability in the presence and abundance of certain wintering birds [e.g., Parids (titmice) and Rufous-sided Towhee (*Pipilo erythrophthalmus*)] was best explained by the habitats in the surrounding landscape (Table 7.3). Other species [e.g., Northern Cardinal (*Pyrrhuloxia cardinalis*) and White-throated Sparrow (*Zonotrichia albicollis*)] responded only to the characteristics of the local habitat, and yet other species [e.g., Carolina Wren (*Thryothorus ludovicianus*)] responded both to local conditions and to the landscape context (Table 7.3).

Many, many subsequent studies have tested for the influence of landscape context and patch-level habitat variables on biodiversity measures. Lindenmayer and Nix (1993) found that the occupancy of corridors by arboreal marsupials in Australia could not be predicted by habitat features within the corridor; information on the composition of the surrounding landscape was required. Winter foraging patterns of elk and bison in northern Yellowstone National Park were explained in part by landscape context (Pearson et al. 1995). Models explaining breeding bird

Table 7.3.
Results of stepwise regression models of bird response variables as explained by within-habitat variables and characteristics of the surrounding landscape

Response variable	Matrix r^2	Model r^2
	Community measures	
Total number of birds	0.24	0.73
Species richness	0.74	0.74
Shannon diversity	0.82	0.82
	Functional groups	
Forest species	0.57	0.84
Early successional species	0.18	0.18
Generalists	0.13	0.73
Parids	0.65	0.76
	Selected species	
Carolina wren	0.48	0.83
Field sparrow	0.24	0.24
Dark-eyed junco	0.24	0.24
Northern cardinal	0.31	0.83
Rufous-sided towhee	0.54	0.83
Song sparrow	0.19	0.19
White-throated sparrow	0.00	0.83

Matrix r^2 reflects the amount of variation explained only by the landscape matrix variables. Model r^2 is the coefficient of determination for the entire regression equation. Amount of variation explained only by within-habitat variables can be computed by difference. From Pearson (1993)

abundance in an urban southern California landscape were significantly improved when landscape variables were added (Bolger et al. 1997). Landscape context also was needed to explain the species richness and abundance of wild bees in southern Lower Saxony, Germany, which were positively associated with the proportion of seminatural habitats and diversity of habitats in the surrounding landscape, and the scale of the effect varied among taxa (Steffan-Dewenter et al. 2002). In general, occupancy or visits to habitat patches are more likely when that habitat type is abundant in the surrounding landscape (Pearson 1993; Lewis et al. 2011); this effect has been documented in many mobile animals, such as mammals, birds, and flying insects that easily move among patches. For species that require a diversity of habitats in the surrounding landscape, patch occupancy or species density may be explained by the mix of patch types that provide supplementary or complementary resources (Dunning et al. 1992).

Landscape heterogeneity also been shown to promote population stability. Empirical data on 35 British butterfly species at 166 different sites revealed that the butterfly populations were more stable in heterogeneous landscapes with a variety of habitat types (Oliver et al. 2010). Furthermore, topographic heterogeneity also appeared to promote stability. As with larger patch sizes, landscapes that have greater heterogeneity may provide a wider range of resources and microclimates that may buffer population fluctuations (Oliver et al. 2010). The key take-home point from these (and many other studies) is that the surrounding landscape often has a strong influence on local populations.

Given the vast number of studies that have been published, have generalities emerged among taxa regarding when and why landscape context matters? Thornton and colleagues reviewed 122 focal patch studies to determine whether the probability of a species responding to the landscape, patch, and within-patch factors varied among taxa and with body size, landscape type, and study methods (Thornton et al. 2011). They found birds to be the most common study species, followed closely by mammals, and herpetofauna were the least common study species. Over half (56 %) of the species included in their review responded to at least one measure of landscape context, similar to the 59 % reported in an earlier study by Mazerolle and Villard (1999). Mammals were more likely to respond to landscape-level variables than were birds, and studies that included a large number of focal patches (i.e., high sample size) were best able to detect such a response. Studies that evaluated characteristics of the surrounding landscape in buffers (e.g., Fig. 7.9) were more likely to detect an effect of landscape context than studies that only used metrics of patch isolation, but the use of multiple buffers did not increase the likelihood of detecting an effect (Thornton et al. 2011), although the magnitude of effects can vary with buffer distance. Species also had a high probability of response to within-patch variables, supporting the influence of fine-scale features of the environment with which species interact most directly (Cushman and McGarigal 2004; Thornton et al. 2011). Interestingly, measures of species density or abundance were more sensitive to within-patch variables than was presence–absence.

Collectively, these examples demonstrate that landscape variables are often key determinants of species' distributions and abundances. This insight is very important for land management because it suggests that what happens in small, local areas is often influenced by the surrounding landscape. Therefore, conservation efforts must consider the characteristics of the surrounding landscape or matrix. For future studies, Thornton et al. (2011) offered several recommendations that merit attention. They argued for (1) reporting standardized effect sizes in focal patch studies to facilitate comparisons among different studies; (2) narrowing the vast set of landscape metrics to a few that are particularly relevant and can be readily applied across studies and ecosystems; and (3) consistent use of a variance partitioning approach that would enable the relative amount of variance explained by predictors at different levels to be compared. Following these guidelines would lead to an enhanced ability to derive generalities from the growing library of empirical studies, which would also feed directly into management recommendations.

The effect of landscape composition on organisms is often stronger than the effect of landscape configuration. As studies of different species in fragmented landscapes accumulated, the question of whether habitat loss or habitat arrangement was driving species' responses came to the fore. Answers differed among taxa and organism responses (e.g., occupancy, abundance, movement, or persistence), but answers also depended on how "habitat fragmentation" was assessed. Many early studies did not separate the effects of composition from those of configuration (see Chap. 4), and as a result, the effect of habitat arrangement relative to overall habitat availability was overestimated. These issues are well described by Lenore Fahrig in an excellent review of habitat fragmentation (Fahrig 2003). As a process that transforms a large expanse of continuous habitat, four effects of habitat fragmentation on habitat pattern are implied: (1) reduction in habitat amount, (2) increase in the number of habitat patches, (3) decrease in the sizes of habitat patches, and (4) increase in the isolation of patches (Fahrig 2003). Fahrig argued persuasively that determining whether habitat fragmentation *per se* has a direct effect on biodiversity depends on whether or not changes in habitat pattern (i.e., an increase in the number of patches with a decrease in patch size) influence species independent of habitat loss within the landscape. Because measures of fragmentation are made at the landscape scale, data at the level of individual patches (i.e., focal patch studies) do not capture the effects of landscape fragmentation. Distinguishing the effects of patch size from the effects of landscape-level habitat fragmentation is difficult but essential (Fig. 7.10), but because these two variables are naturally confounded inappropriate study designs (and analysis) can lead to incorrect conclusions. The merging of composition and configuration effects in many habitat fragmentation studies has obscured the fact that the effects of total habitat loss far outweigh the effects of fragmentation per se (Fahrig 2003).

The studies reviewed by Fahrig (2003), as well as many other studies, have clearly demonstrated negative effects of habitat loss on biodiversity metrics including species richness, population abundance and distribution, genetic diversity, and even breeding success and population growth rate. The question is then how fragmentation of habitat affects biodiversity independent of habitat loss. *Fragmentation* per se refers to the effects of breaking apart of a given amount of habitat, or in other words, a change in spatial configuration after controlling for habitat amount (Fig. 7.11). Negative effects of habitat fragmentation can be attributed primarily to two effects. First, fragmentation implies a larger number of smaller patches, and at some point, patches get so small that a local population cannot be sustained.

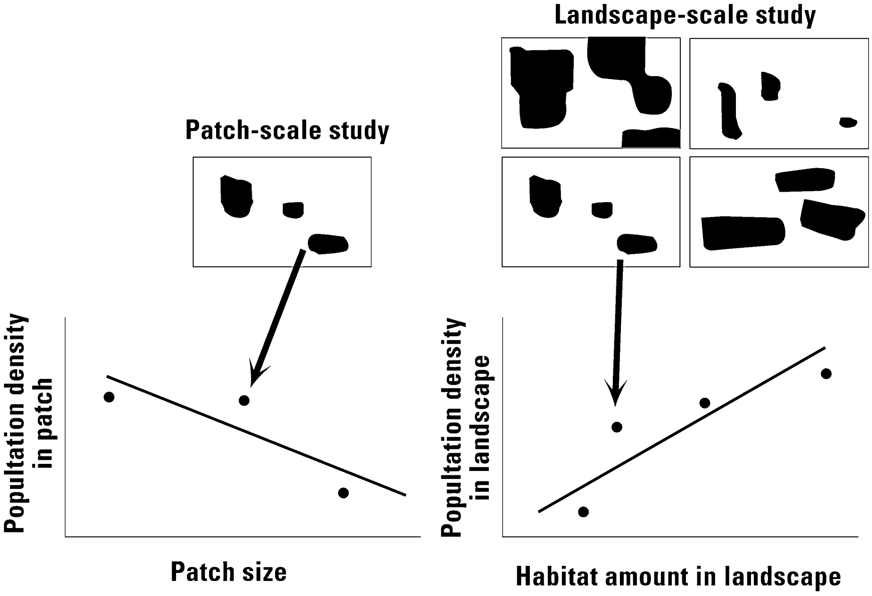


FIGURE 7.10.
(**a**) Patch-scale study. Each observation is represented by a single patch in a single landscape, so landscape-scale inference has $n = 1$. (**b**) Landscape-scale study. Each observation represents information from a single landscape, and multiple landscapes are studied. Here, $n = 4$.

ADAPTED FROM FAHRIG (2003)

Second, edge effects can have a negative influence on populations, such as the well-known increase in predation and nest parasitism on forest birds along patch edges (Gates and Gysel 1978). Surprisingly, Fahrig (2003) also found evidence for positive effects of habitat fragmentation, which may emerge from the stabilizing influence of spatial heterogeneity may have on species interactions or single-species populations.

Large field experiments complement observational studies by providing appropriate controls for pattern variables (e.g., patch number, area, and size) that are naturally confounded when fragmentation occurs (Ewers et al. 2011). For instance, the Savannah River Site Corridor Experiment manipulated landscape pattern to compare isolated versus connected designs while controlling for total habitat area (Haddad 1999a, b; Damschen et al. 2006). Results found that habitat patches connected by corridors retain more native plant species, but edge effects determine movement of air-borne plant pathogens (Johnson and Haddad 2011). An experiment studying insect dispersal was conducted at finer scales by With et al. (1999) using landscape-level designs based on fractal algorithms to vary edge effects while holding the overall proportions of grass and bare ground constant. The results showed a threshold response of dispersal based on insect body size, with grassy areas providing cover and sandy areas allowing rapid dispersal. Ewers et al. (2011) described the

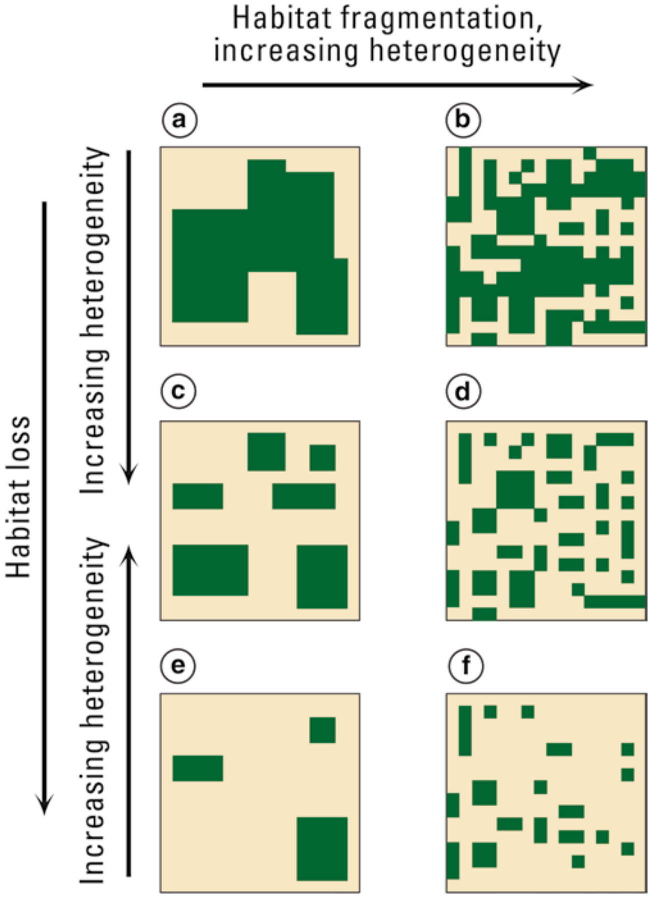


FIGURE 7.11.
Habitat loss and habitat fragmentation are distinct. In these hypothetical landscapes, habitat amount declines from *top* to *bottom*. In each row, habitat amount is constant, but fragmentation increases from *left* to *right*.

ADAPTED FROM FAHRIG AND NUTTLE (2005)

design criteria for a new forest fragmentation experiment to be initiated in lowland tropical forests of Borneo that will allow discrimination of landscape-level forest cover from patch-level processes, facilitate collection of a wide range of data types, increase replication relative to existing experiments, include manipulation of riparian corridors, and embed the study in a wide gradient of land-use intensity. While experimental approaches are essential, relatively few large experimental studies have been conducted because they are costly to perform and difficult to replicate.

Landscape composition strongly influences landscape connectivity. Landscape connectivity refers to the degree to which the landscape facilitates or impedes movement among resource patches (Dunning et al. 1992). While conceptually simple, quantifying landscape connectivity continues to be a challenge (Calabrese and Fagan 2004). Although connectivity metrics abound (e.g., Kindlmann and Burel 2008; Prugh 2009), direct observation of movement is difficult for many species and often impossible when large areas must be monitored. Thus, many studies have relied on assessments of *structural connectivity*, the degree to which landscape elements are contiguous, or physically linked, to one another. *Functional connectivity* considers the actual movement or dispersal of organisms and is the degree to which movement occurs. It is important to distinguish potential or structural connectivity from actual or functional connectivity (Bélisle 2005). As with patch occupancy, connectivity in the landscape can be strongly influenced by the surrounding matrix, that is, the areas that are not the habitat of interest. There are at least three important roles of the matrix on connectivity (Murphy and Lovett-Doust 2004). (1) The matrix may either reduce or enhance dispersal and colonization rates. (2) The matrix may provide alternative, though perhaps suboptimal, habitat for the population. (3) The matrix may be a source of novel invading species that compete with the focal population for patch space, prey on the focal species, or provide a resource.

An example of how land-cover change can affect organism movement and alter landscape connectivity comes from studies of the poison-dart frog, *Oophaga pumilio*, in and near the La Selva Biological Station in Costa Rica (Nowakowski et al. 2013). As a group, amphibians can be especially sensitive to landscape changes, such as forest clearing, which increase their vulnerability to dessication or predation risk and/or alter the physical permeability of the vegetation to movement. The colorful poison-dart frog is a common species often found in lowland and wet forests, including tree plantations. Experimental studies of the poison-dart frog revealed increased resistance to movement (i.e., reduced connectivity) in pastures compared to secondary forests (Nowakowski et al. 2013). Pastures are hotter and drier, providing inhospitable microclimate conditions for the frog, and the authors suggest predation rates are also higher in pastures. Further, movement orientation was strongly directional toward forest and away from open habitat when frogs were placed in pasture locations that were within 50 m of a forest edge. Movement orientation was random in undisturbed forests and in pastures >50 m from forest, which was probably beyond the perceptual range of the frog (Nowakowski et al. 2013). In this fragmented forest landscape, the poison-dart frog must often travel across a matrix of semipermeable pastures to move among forest habitat patches.

A study of a Neotropical understory frugivorous bat (*Rhinophylla pumilio*) in French Guiana provides an excellent example showing the relative importance of functional landscape connectivity and local resources on bat abundance (Henry et al. 2007). Using a 10-year bat mist-net survey coupled with local estimates of food availability, Henry et al. monitored bat use of 18 sampling sites ranging from undisturbed forest communities to small, remote forest fragments. They assessed connectivity based on the amount of forest cover in the landscape surrounding each site and used radio-tracking data to weight these forest areas by the probability that bats would use them. The results of the study showed that abundance of *R. pumilio* was positively correlated with landscape connectivity, but not correlated with local food availability (Henry et al. 2007).

Habitat connectivity is related to habitat abundance and can be a threshold phenomenon (see Chap. 3). Andren (1994) reviewed the empirical evidence for birds and mammals that could be used to test predictions derived from neutral landscape models regarding habitat connectivity. He examined habitat fragmentation, including the combined effects of loss of habitat, reductions in patch sizes, and increased distances between patches. His results led to the conclusion that the relative importance of these three habitat characteristics differs as a function of the total abundance of suitable habitat in a landscape. When landscapes have >30 % suitable habitat, the primary effect on habitat connectivity is habitat loss. This is because in landscapes with relatively high proportions of suitable habitat, the habitat is reasonably well connected while its configuration is less important. In experimental landscapes designed to study beetle movement, Wiens et al. (1997) found threshold effects when grassy habitat was less than 20 %. Simulations conducted by Fahrig (1997) also demonstrated that the effects of habitat loss could outweigh the effects of habitat fragmentation on population extinction. In landscapes with low proportions of suitable habitat (10–30 %), the spatial arrangement of patches was very important. Further reduction in habitat resulted in an exponential increase in distances between patches, that is, rapid decreases in connectivity; With and King (1999a) found evidence for a strong effect of gap structure on dispersal success. Moreover, the effect of patch size and isolation depends not only on the proportion of original habitat in the landscape, but also on the suitability of the surrounding habitats (e.g., the matrix, areas between "patches") for movement. Indeed, the results from both the theory and empirical studies suggest that conservation actions, such as adding habitat or protecting key locations, are most likely to have substantial effects on habitat connectivity when the suitable habitat is relatively low in abundance (Andren 1994; Pearson et al. 1996; Fahrig 1997). It is in this range where small changes in habitat abundance are likely to cause the threshold of connectivity to be passed. It is important to recognize that the effects of habitat loss cannot be mitigated simply by connecting remaining habitat fragments—but enhancing connectivity can help, and corridors have become cornerstones of modern conservation (Chetkiewicz et al. 2006).

Corridor creation can both add habitat and promote movement. *Corridors* are regions of the landscape (typically narrow strips of habitat) that connect otherwise isolated habitat patches and facilitate the flow or movement of individuals, genes, and ecological processes. The primary purpose of corridors was to counter the consequences of habitat loss and fragmentation, although corridors were also thought to provide routes and habitats for organisms moving in response to climate change (Chetkiewicz et al. 2006). Corridors are assumed to increase population persistence by providing for an exchange of individuals among a population that was previously connected but which is now fragmented. Because corridors may be strongly influenced by edge effects, interior habitat is often minimal and may even be absent completely in corridors. Corridors are intuitively appealing, but empirical evidence that documented whether and how corridors function lagged behind implementation, and there has been much discussion regarding their effectiveness (e.g., Simberloff and Cox 1987; Saunders and Hobbs 1991; Hobbs 1992; Beier and Noss 1998; Damschen et al. 2006).

Rosenberg et al. (1997) provided a useful distinction between two functions of linear landscape features: (1) corridors may themselves provide habitat, containing the resources needed for survival, reproduction, and movement, and thus augment habitat area; or (2) corridors may augment connectivity, providing for movement between habitat patches but not necessarily for population persistence. Rosenberg et al. (1997) synthesized the literature and identified a set of common patterns about corridor effectiveness. First, when confronted by a choice, individual animals were likely to select pathways for movement that included components of their habitat, and this behavior was most pronounced for individuals moving within their home range. Second, the relative use of the matrix for movement depended on its contrast with the organism's suitable habitat. Third, animal behavior could change in areas of less favorable habitat; e.g., animals may move more rapidly when traversing low-quality habitat than in high-quality habitat. Many questions remained, however, and subsequent studies have yielded more understanding of the function of landscape corridors (e.g., see Chetkiewicz et al. 2006; Gilbert-Norton et al. 2010).

Recent experimental studies have been particularly instructive. For example, Sharon Collinge (2000) conducted an experimental study of grassland patches within a matrix of mowed vegetation and tested for effects of corridors on arthropod communities. Corridor effects on insect diversity were weak, perhaps because the patch and matrix habitats had relatively low contrast, and the insect species had relatively high capacity for dispersal, suggesting a broader scaling of the landscape. In a forest matrix, the Corridor Experiment at the Savannah River Site in Aiken, South Carolina, has tested for effects of corridors on a wide range of species and responses while controlling for habitat area and patch shape (e.g., Haddad 1999b; Haddad et al. 2003; Fig. 7.12). The first experiment examined the effect of connecting habitat patches, which were openings in the forest matrix, by nonforest corridors of different length. There was increased movement of birds, plants, butterflies in open patches that were connected by a corridor, along with increased density and gene flow for some butterfly species. These studies suggested that corridors do indeed promote movement or organisms among patches, and a recent review indicated that corridors increased interpatch movement by about 50 % compared to movement between isolated patches (Gilbert-Norton et al. 2010).

The second experiment at the Savannah River Site was designed to evaluate the mechanisms of movement along corridors joining adjacent patch areas, i.e., were effects due to habitat area, patch shape, or connectivity? Eight experimental landscapes were established with each centered on a 1-ha open habitat patch. By adding the area included in corridors to unconnected patches, the effect of area alone could be considered. By extending dead-end "wings" from the central patch, the effect of additional edge habitat that did not lead to another patch could be considered. The results showed that corridors increased the movement of birds, plants, and butterflies (e.g., Levey et al. 2005; Tewksbury et al. 2002; Haddad and

Figure 7.12.
Aerial view of the corridor experiment that was established at the Savannah River Site, Aiken, NC
(Photo by Ellen Damschen)

Tewksbury 2005); increased density of three butterfly species (Haddad and Baum 1999); and enhanced gene flow for one butterfly species (*Junonia coenia*) (Wells et al. 2009). Interspecific interactions were also affected. For example, seed predation by small mammals increased in connected patches, but seed predation by invertebrates increased. The fate of wind-dispersed seeds was affected by both patch shape and connectivity. The net effect of corridors on plant community diversity was an increase in plant species richness in connected vs. unconnected patches, and the difference increased over time (Damschen et al. 2006). Current research priorities include elucidating the roles of corridor quality and the habitat matrix on movement, and understanding how corridor width may influence functional connectivity (Damschen 2013).

Synthesis: when is spatial pattern important? The effect of spatial heterogeneity on organisms, while interesting in its own right, certainly adds a substantial degree of complexity to population or community studies. But when is space really important and when might spatial relationships be prudently ignored? It is absolutely critical to account for habitat amount when considering the effect of habitat configuration (including edge effects) on any population response. Spatial pattern (i.e., configuration) is likely to matter most when habitat is relatively scarce and matter less when habitat is abundant. Spatial pattern will also matter when edge effects influence organisms (e.g., Johnson and Haddad 2011) because edge:area ratios vary with patch size and shape. Spatial patterns will also be important if habitat arrangements limit organism movements between patches and if a population is characterized by metapopulation dynamics. From this, we can infer that spatial considerations may not be needed if habitat is very abundant or if movement is relatively unlimited, allowing organisms to reach nearly all areas containing suitable habitat. Finally, it is essential to recognize the limitations of a strictly patch-based view of the world that ignores the nature of the landscape matrix and to know when a more complete or continuous view of spatial heterogeneity is required. Spatial pattern will matter if landscape context explains variation in population metrics among sites. Franklin (1993) argued that conservation considerations should include both a patch-based component, such as the design (size and spacing) of nature reserves, as well as assessments of the condition (and management) of the matrix, i.e., the intervening areas between patches or reserves. For an excellent summary that includes hypotheses for when landscape heterogeneity influences biodiversity (Table 7.4), we also refer readers to Tscharntke et al. (2012).

TABLE 7.4.
EIGHT HYPOTHESES PROPOSED BY TSCHARNTKE ET AL. (2012) FOR HOW LANDSCAPE HETEROGENEITY MAY INFLUENCE BIODIVERSITY PATTERNS AND PROCESSES

Hypothesis name	Hypothesis statement
Landscape species pool	The size of the landscape-wide species pool moderates local (alpha) biodiversity
Dominance of beta diversity	The landscape-moderated dissimilarity of local communities determines landscape-wide biodiversity and overrides negative local effects of habitat fragmentation on biodiversity
Cross-over habitat spillover	Landscape-moderated spillover of energy, resources, and organisms across habitats, including between managed and natural ecosystems, influences landscape-wide community structure and associated processes
Landscape-moderated concentration and dilution	Spatial and temporal changes in landscape composition can cause transient concentration or dilution of populations with functional consequences
Landscape-moderated functional trait selection	Landscape moderation of species functional trait selection shapes the functional role and the trajectory of community assembly
Landscape-moderated insurance	Landscape complexity provides spatial and temporal insurance, i.e., higher resilience and stability of ecological processes in changing environments
Intermediate landscape-complexity hypothesis	Landscape-moderated effectiveness of local conservation management is highest in structurally simple, rather than in clears (i.e., extremely simplified) or in complex landscapes
Landscape-moderated biodiversity vs. ecosystem service management	Landscape-moderated biodiversity conservation of endangered species will not optimize functional diversity and related ecosystem services in production systems

LANDSCAPE HETEROGENEITY AND SPECIES INTERACTIONS

Early work in landscape ecology elucidated how species presence, richness, and abundance varied with landscape composition and configuration. More recently, researchers have extended this line of inquiry by delving into how biotic interactions and community distributions may be influenced by landscape heterogeneity. For instance, in fragmented forests of the Pacific Northwest, elevated densities of deer mice (*Peromyscus maniculatus*) in clear-cuts were associated with reduced recruitment of trillium (*Trillium ovatum*) because of greater seed predation by these mice within clear-cuts (Tallmon et al. 2003). Thus, a prescribed cutting pattern of forested landscapes resulted in shifts in biotic interactions that subsequently altered population dynamics. We next consider research that moves beyond single populations.

Predator–Prey Interactions

One exciting research topic is determining how landscape heterogeneity mediates *predator–prey interactions*, which affect population dynamics and community structure in many landscapes (Abrams et al. 1996; Schmitz 1998). Although this topic has long been a focus in theoretical population ecology, predator–prey interactions in the real world take the form of a dynamic game played in spatially complex landscapes. Outcomes for the prey and the predator—being eaten or getting a meal—are affected by what other players do and the setting in which interactions occur. Thus, empirical predator–prey studies expanded to consider explicit space (e.g., Fauchald et al. 2000; Kunkel and Pletscher 2001; Phillips et al. 2004; Hernández and Laundré 2005). Studies have evaluated patterns of space use and movements of predators and prey in concert to explain their co-occurrence on the landscape and the patterns of predation that result. But why does space matter?

Landscape patterns can influence the probability of prey encounters and kills (Hebblewhite et al. 2005) and the effectiveness of antipredator strategies (Andruskiw et al. 2008). Landscape attributes (such as habitat type, habitat connectivity, patch size, and topographic setting) can render prey more or less susceptible to predation, and effects of the landscape can differ between the encounter and attack stages of predation (Hebblewhite et al. 2005). Further, landscape locations where prey are most likely to be encountered by predators may not coincide with areas where prey are most likely to be killed. Using a wolf–elk study system in Banff National Park, Canada, Hebblewhite et al. (2005) found strong evidence for an influence of the landscape—for example, the odds of elk being encountered by wolves were 1.3 times higher in pine forest and 4.1 times less in grasslands than in other habitats. They then combined the probability of encounter and conditional probability of death into a spatially explicit function of predation risk. However, prey may need to use risky locations because safe patches may not provide adequate food or other resources. This need for prey to use high-risk patches ultimately drives the predator–prey system in a heterogeneous landscape, and it is in those high-risk areas that "the deadly game of stealth and fear is played out" (Laundré 2010).

A 16-year telemetry study of a one-predator–one-prey system of pumas (*Puma concolor*) and mule deer (*Odocoileus hemionus*) in southern Idaho and northwestern Utah, USA, provides a useful example of predator–prey dynamics in a complex landscape. Laundré (2010) tested a set of predictions regarding predator–prey distributions and patch use by the predator. The landscape consisted of various-sized forest and open areas with low shrubs and grasses. The open areas are rich in mule deer forage and relatively safe from puma predation, as pumas require stalking cover and are more successful along forest edges and within forest patches. However, forest patches can provide mule deer with protection from heat during summer and from wind and cold during winter; thus, deer move between relatively safe open patches and riskier forest patches. The study clearly showed that pumas and deer do not use forest patches at random. Pumas used large forest patches more than expected, revisited individual large patches more than smaller ones, and remained longer in larger patches than in smaller ones. Deer spent more time farther from the forest edge than along the edge, and at night, when deer were feeding and pumas were hunting, deer spent most of their time in the low-risk open areas. The results demonstrated a negative relationship in the spatial distribution of the predator and prey, with each player selecting habitat elements that give it the advantage (Laundré 2010). Laundré concluded that, within a heterogeneous landscape, who "wins" the predator–prey game depends on where you are; deer "win" in open areas; pumas "win" in forest edges. The overall outcome will depend on the relative amounts and arrangements of safe and risky habitats. Laundré (2010) posits that, if a landscape is predominantly safe habitat, the prey's response will dominate, and high prey densities and prey:predator ratios are expected. If risky habitat predominates, then prey densities and prey:predator ratios will be lower (Laundré 2010). These and other studies are generating exciting new insights into how the composition and configuration of landscapes can have a surprisingly strong influence on the interactions between species.

In many locations, prey face multiple predators and must evaluate complex patterns of predation risk as they use the landscape. In the Karongwe Game Reserve, South Africa, Thaker et al. (2011) examined the distribution of seven African ungulate species as a function of predation risk from all larger carnivore species (lion, leopard, cheetah, African wild dog, and spotted hyena). They used kill data to generate predictions, for each species of ungulate, of the relative predation risk of different habitats. They tested five different hypotheses of strategies that would reduce the probability of encountering predators and the probability of being killed (Table 7.5). Results demonstrated that ungulates distinguished among different potential predators and were distributed across the landscape in ways that simultaneously minimized predation risk from multiple predators (Thaker et al. 2011).

TABLE 7.5.
HYPOTHESES OF HOW UNGULATES CAN AVOID PREDATION RISK IN A LANDSCAPE OF MULTIPLE PREDATORS THAT WERE TESTED FOR SOUTH AFRICAN UNGULATES AND THEIR PREDATORS

Hypotheses	Ungulates found to use this strategy
Strategies that reduce the probability of encountering predators	
1. Ungulates avoid areas that are heavily used by their main predators (those with the highest contribution to prey mortality)	
2. Ungulates avoid areas that are heavily used by all predators	Warthog, impala, waterbuck, kudu
3. Ungulates avoid areas that are heavily used by sit-and-pursue predators (lion, leopard), more than they avoid areas used by less predictable cursorial predators (African wild dog, cheetah)	Wildebeest, giraffe, zebra
Strategies that reduce the probability of being killed	
4. Ungulates avoid risky habitats, where the probability of kills is high	Warthog, impala, wildebeest, giraffe, zebra
5. Ungulates select safer habitats, where the probability of kills is low	Wildebeest, giraffe, zebra, waterbuck

ADAPTED FROM THAKER ET AL. (2011)

Prey selected locations that reduced the probability of encounter with a predator as well as the probability of being killed. Ungulate antipredator strategies also varied with body size; smaller prey avoided areas used by all predators, whereas larger prey avoided areas that were often used by lions and leopards (Thaker et al. 2011).

Nonlethal interactions between species can be as important as predation events in affecting how species use a landscape (Peacor 2002; Schmitz et al. 2004; Creel et al. 2005; Werner and Peacor 2006). Prey may perceive the presence of predators through various senses (hearing, smelling, seeing), even in the absence of actual kills, and thus respond to *landscapes of fear* (Brown et al. 1999; Laundré 2010). In landscapes where predators are territorial, prey can avoid areas of high predator activity by using portions of the landscape that are outside or near the boundaries of predator territories. In a reintroduced and expanding population of elk (*Cervus elaphus*) in northern Wisconsin, elk home-range establishment during summer was largely explained by the spatial distribution of wolf territories; elk established home ranges at the boundaries of wolf territories and avoided the centers (Anderson et al. 2005), even though the wolves were preying upon deer rather than elk.

Understanding the spatial context of predation has important implications for conservation. Landscape conservation strategies that do not account for landscape influences on predator behavior and subsequent sifts in predator–prey dynamics may be ineffective at protecting the prey species. For example, various landscape management strategies have been developed to mitigate the effects of human activities, such as forest harvesting, on woodland caribou (*Rangifer tarandus caribou*) populations, but most plans do not account for wolves, their primary predator. One management plan developed in Quebec, Canada, protected large areas of forest and spatially aggregated forest harvests. To determine how that landscape plan might affect wolf predation on caribou, Courbin et al. (2009) modeled the spatial relationships of each species with their habitat, then estimated their co-occurrence in the landscape. The highest probability of wolf–caribou co-occurrence during winter and spring was in the protected forests. The authors recommended that management consider habitat selection by both species and, to conserve caribou, protect areas that included mature conifer forests with lichen, minimized mixed and deciduous forest stands, and were distant from roads and cut blocks (Courbin et al. 2009). More generally, they emphasized the need to incorporate predator behavior into management plans for long-term persistence of prey that are strongly affected by top-down control.

The spatial implications of trophic cascades (Pace et al. 1999) also suggest the potential for spatially dependent consequences of altered behavior and/or numbers of herbivores to affect plant communities. When top-down control operates, the presence of predators may reduce herbivore numbers and release plants from herbivory. In a landscape, such responses would be expected to occur in high-risk locations that might be avoided by foragers. For example, researchers hypothesized that elk herbivory on preferred woody species, such as aspen and willow in Yellowstone National Park, would be reduced by a numerical decline in elk population size or a behavioral response following the reintroduction of wolves in 1995 (National Research Council 2002). Many studies were initiated to evaluate this potential trophic cascade at the landscape level. Although a *behaviorally mediated trophic cascade* (*BMTC*) leading to aspen and willow recovery is intuitively appealing, different studies have reported different outcomes (Kauffman et al. 2010; Ripple and Beschta 2012; Winnie 2012). After 10 years, an analysis of kill-site locations in northern Yellowstone showed a strong influence of landscape factors on predation (Kauffman et al. 2007). However, whether these patterns translate to recovery of vegetation is less clear. For example, Creel and Christianson (2009) found increased willow consumption in the presence of wolves, but Beyer et al. (2007) found increased willow growth in the presence of wolves. For aspen, Ripple and Beschta (2012) argue for a BMTC, whereas other authors suggest not (e.g., Kaufmann et al. 2010). Winnie (2012) evaluated specific hypotheses associated with a BMTC involving predation risk, elk and aspen, and found no evidence that aspen were responding to risk factors in ways consistent with the BMTC. His thorough review of published literature focused on vegetation dynamics following wolf reintroduction in Yellowstone (Winnie 2012) also underscores the critical need to develop and testing competing hypotheses consistent with the mechanisms that underpin landscape-level responses along with the need for rigorous, long-term study.

Natural Enemies and Pollination in Agricultural Landscapes

Predator–prey interactions in heterogeneous landscapes have also been considered for insects, particularly in agricultural landscapes where predators may be *natural enemies* that help to keep crop pests in check (Tscharntke et al. 2007). Noncrop habitat can provide alternative foods and shelter for mobile arthropods that prey on crop pests, and thus conserving noncrop habitats may enhance beneficial species interactions in heterogeneous agricultural landscapes. Research has demonstrated that natural enemies are more diverse and numerous in landscapes with abundant natural or seminatural habitat compared to more homogeneous, intensively cultivated landscapes (e.g., Chaplin-Kramer et al. 2011). However, relatively few studies have assessed the effect of landscape context on such trophic interactions.

To evaluate the relative effect of local and landscape factors on pest predation, Werling and Gratton (2010) studied predation of two insect pests of potatoes, the Colorado potato beetle (*Leptinotarsa decemlineata*) and green peach aphids (*Myzus persicae*). These are important pests of potatoes in Wisconsin, USA, and both are attacked by a diverse assemblage of arthropod predators. These authors quantified predation in 50 widely distributed potato fields and evaluated the influence of local grassy field margins and landscape composition within 1.5 km of each potato field. The results varied between the pest species. Predation on the Colorado potato beetle was affected by grassy field margins but was unaffected by landscape context. In contrast, predation on green peach aphid was affected by landscape context, increasing with the amount of noncrop habitat in the surrounding landscape, but was less affected by habitat along field margins (Werling and Gratton 2010). The different responses for the two pest species suggest the importance of conserving noncrop habitats at a variety of scales in agricultural landscapes (Werling and Gratton 2010). Research on cavity-nesting bees, wasps, and their enemies in 30 farmland sites in the Swiss Plateau yielded similar findings (Schüepp et al. 2011). Their study focused on cherry orchards embedded in landscapes that varied in composition within a 500-m radius and were isolated to varying degrees. The species richness of wasps increased with more woody habitat in the surrounding landscape, but wasps and natural enemies were reduced in abundance with increasing patch isolation. There was no significant effect of landscape variables on species richness of bees. Parasitism rates declined with increasing isolation, suggesting that isolation could release arthropods from control by natural enemies (Schüepp et al. 2011).

Landscape pattern can also affect the interactions among natural enemies, leading to unexpected consequences for pest predation. In an experimental study that included three natural enemy guilds (birds, flying insects, and ground-dwelling arthropods), Martin et al. (2013) evaluated the role of landscape context on pest densities and crop yield. Their results seemed surprising at first because herbivore (pest) pressure was *greater* rather than less in landscapes with more seminatural habitats. However, this response resulted from interactions among the natural-enemy guilds. Landscape context had no effect on pest predation by birds or ground-dwelling insects, but it did influence predation by flying insects. Pest predation by flying insects increased with the percentage of seminatural habitat in the surrounding landscape (Martin et al. 2013). When looking at the trends more closely, when there was >25 % seminatural habitat in the surrounding landscape and birds were present, there was a decline in pest reduction by flying insects (Fig. 7.13). These results suggest that bird predation on flying insects increased in the more diverse landscapes, which in turn reduced pest control by the flying insects (Martin et al. 2013). Thus, complex landscapes may benefit generalist, fourth-trophic-level enemies more than specialist third-trophic-level enemies. This study also highlights opportunities for further unraveling complex trophic cascades in heterogeneous landscape.

Pollination is another biotic interaction that can show strong effects of landscape heterogeneity (Kremen et al. 2007). In coffee plantations in Costa Rica, species richness of bees, visitation rate, and pollen deposition rate were greater in sites within 100 m of forest fragments than in sites that were farther away

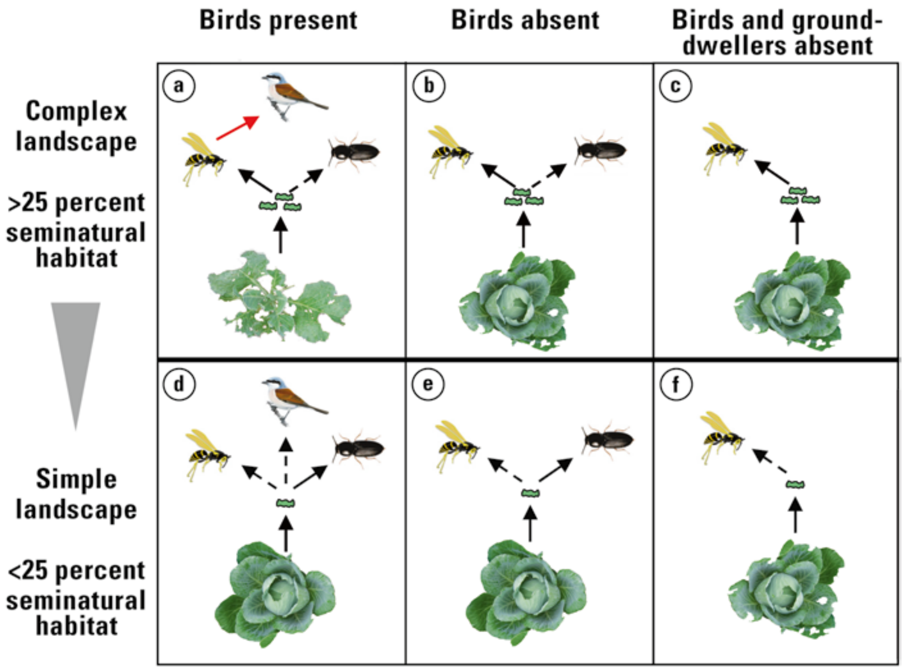


FIGURE 7.13.

Summary of landscape effects on trophic interactions between natural enemies and their consequences for plant herbivory. (**a–c**) Damage in complex landscapes with >25 % seminatural habitat where herbivore pressure is strong. (**d–f**) Damage in simple landscapes where herbivore pressure is low. See text for explanation.

FROM MARTIN ET AL. (2013)

(Ricketts 2004). In organic and conventional watermelon (*Citrullus lanatus*) farms situated along a gradient of isolation from natural habitat in California, USA, pollination services from native bees increased with the proportion of upland natural habitats surrounding farms (Kremen et al. 2004). Honeybees are the dominant pollinator of watermelon in that landscape, and the scale of the relationship matched honeybee foraging ranges. Furthermore, the stability and predictability of pollination services increase with the natural habitats in the surrounding landscape. A practical application of this kind of information is that land-use planners could establish conservation targets for natural habitats that would help to maintain pollination in the agricultural landscape.

Community Structure

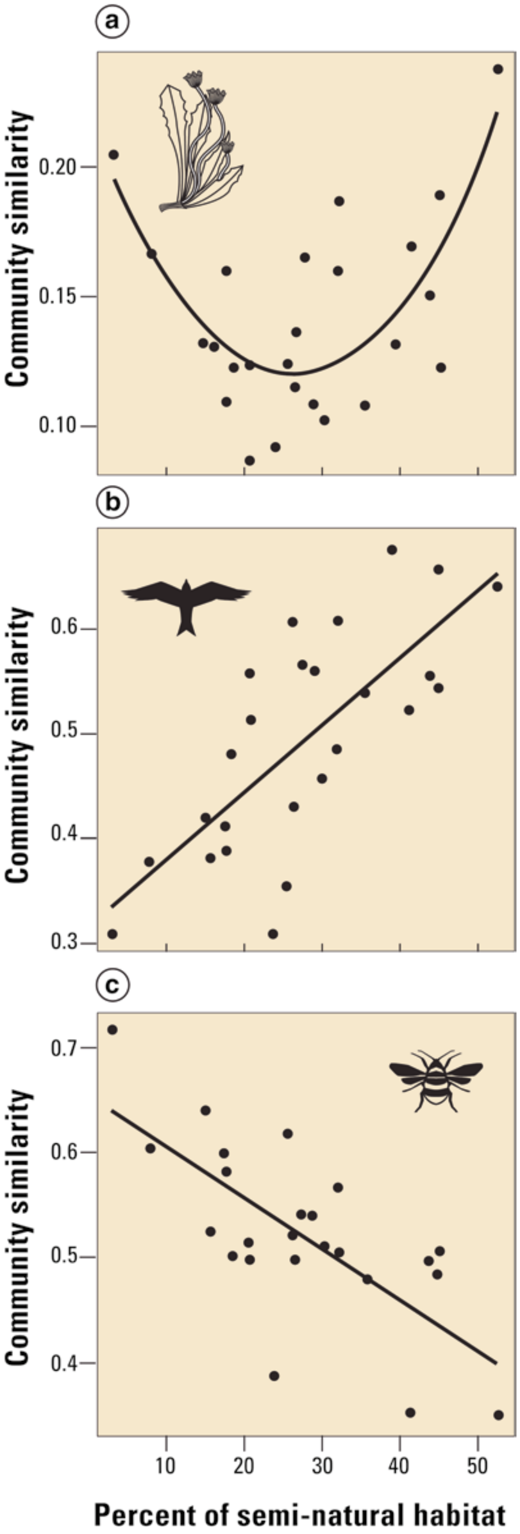
Population interactions imply community-level responses, and landscape ecology studies have indeed begun to evaluate landscape influences on biotic community structure. Such studies grew out of earlier patch-based analyses of species richness and a growing appreciation of how landscape context can influence species interactions. At the community level, these questions focus on how community composition varies with landscape and local influences.

Along a transect extending from France to Estonia, Carsten Dormann along with many colleagues asked whether species turnover and community similarity were affected by landscape structure and local land-use intensity (Dormann et al. 2007). They measured the similarity of plant, bird, wild bee, true bug, carabid beetle, hoverfly, and spider communities sampled along gradients of landscape composition (such as the amount of seminatural habitat), landscape configuration, and land-use intensity. Their results showed a strong effect of the extent of seminatural habitat in the landscape on plant, bird, and bee communities (Fig. 7.14). Plant communities were most similar in homogenous and more fragmented landscapes, whereas bird community similarity increased and wild bee community similarity decreased in landscapes with more seminatural habitats. Furthermore, more intensive local land use led to more homogenous bee, bug, and spider communities within sites, indicating an interaction between landscape and local conditions. The overall patterns for these different biotic communities indicated reduced exchange of species between communities in landscapes dominated by agriculture (Dormann et al. 2007). Interestingly, and related to the discussion of corridors, Dormann et al. (2007) suggested that planting linear elements (e.g., hedgerows) in intensively used landscapes will yield little benefit because they produce little increase in the total area of seminatural habitat. In such landscapes, increasing the total area of seminatural habitat is more important. In contrast, in less intensively used landscapes with more seminatural habitat, increasing connectivity per se would be more advantageous.

Research on plant-community change has produced novel insights about the relative importance of landscape drivers in shaping community structure and whether

Figure 7.14.
Community similarity in different taxa as a function of percent seminatural habitat in European landscapes from France to Estonia.

Adapted from Dormann et al. (2007)



the role of landscape drivers changes over time. Remeasurement of permanent vegetation plots can be used to track temporal changes in the abundance and distribution of species and to evaluate changes in the variables that explain patterns of change in community assemblages. In Wisconsin, USA, the eminent plant ecologist, John Curtis, sampled hundreds of vegetation plots ca. 1950 to develop a quantitative description of the state's plant communities (Curtis 1959). By 1950, much of this landscape had already been converted to agriculture, and forest fragments were patchily distributed in a matrix of crops, pasture, and urban development (Curtis 1959; see Fig. 4.1) The Curtis data archive has provided a baseline for assessing long-term (40–55 years) vegetation change in a variety of plant communities. Plant ecologists relocated upland forest plots that Curtis originally sampled between 1948 and 1951 and followed identical methods to resample the vegetation between 2002 and 2005 (Rogers et al. 2008, 2009). Between 1950 and 2005, the forest canopy shifted from mostly oaks (*Quercus* spp.) to more mesic, shade-tolerant species, primarily maples (*Acer* spp.; Rogers et al. 2008). Understory species diversity declined substantially (~25 %), woody species increased relative to herbaceous species, and the plant communities became more homogenous. These data were then analyzed to determine whether patch size, isolation, and urbanization predicted shifts in native species richness, heterogeneity, and composition (Rogers et al. 2009). Landscape variables were calculated within buffers of 1, 2, and 5 km around each vegetation plot (Fig. 7.15). Results were striking; for the herbaceous community, the strength of correlation with local environmental factors declined sharply from 1950 to 2005 while correlations with landscape variables increased. Patch characteristics of size, proximity, and percent forest cover within 5 km were not correlated with native species in 1950, but all were correlated in 2005. Species losses were greatest in small patches with less forest in the surrounding landscape (Rogers et al. 2009). Further, colonization by new species was lower in sites surrounded by high road densities and more urban cover. The study demonstrated that local site conditions may be insufficient to predict current (or future) plant community composition, and that the relative importance of landscape structure in explaining community composition can shift over time.

Historical land use can shape contemporary plant communities, even altering the among-site variability in plant communities. Declines in local (alpha) diversity in forest growing on former agricultural lands has been well described (cf. Chap. 2), but few studies had examined composition differences among sites (beta diversity). In a study using 11 distinct data sets of forest plant distributions in ancient and recent forests in Europe and North America, Vellend et al. (2007) demonstrated decreases in beta diversity and a weakening of the species–environment relationships in recent forests. Because environmental variability did not differ between the forest types, the authors attributed the declines in beta diversity to constraints on dispersal into the recent forests (Vellend et al. 2007). Thus, the "ghost of land use past" was influencing community diversity not only within but also among sites, long after agricultural land use had ceased.

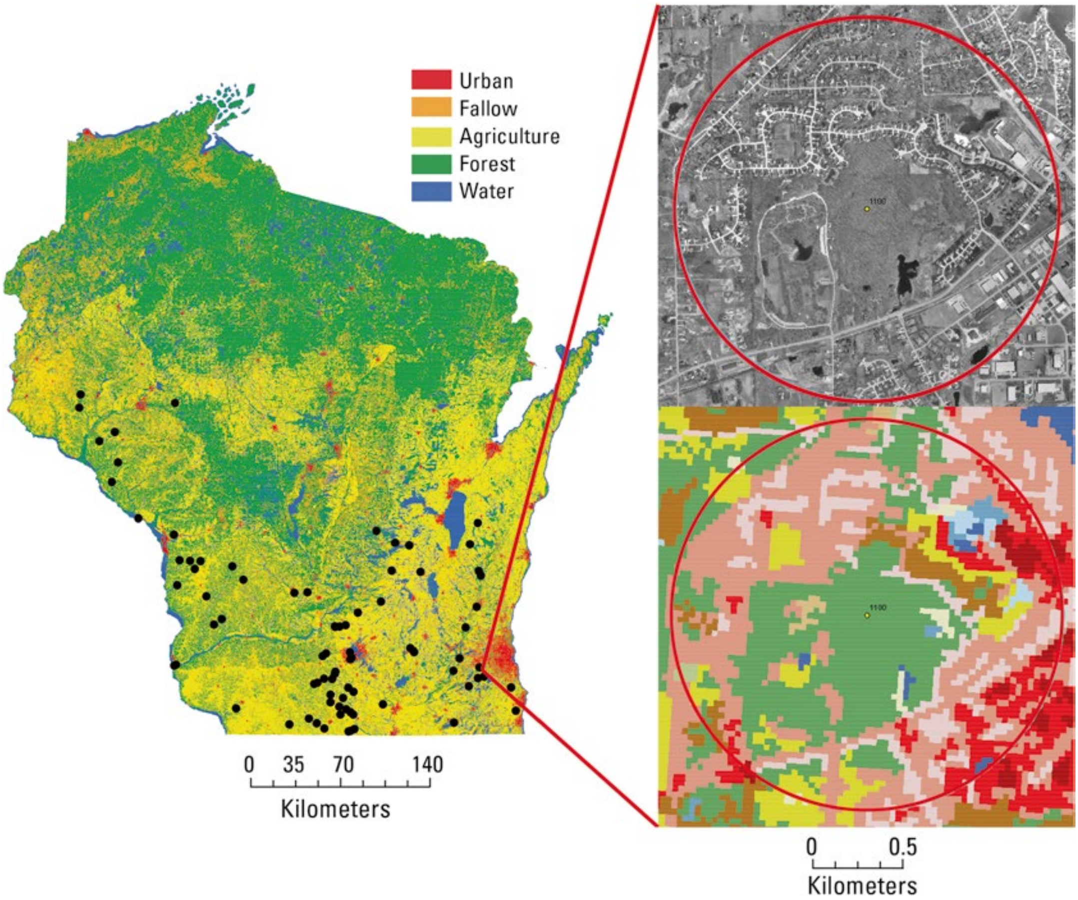


FIGURE 7.15.
Locations of 82 sites in Wisconsin, USA, and views of single site with 1-km buffers used to calculate 2000-era road and housing density (*black and white aerial image*) and land cover (*lower color image*) to explain changes in species composition.

FROM RODGERS ET AL. (2009)

In sum, species interact with each other in heterogeneous landscapes, and such interactions and the community structure they produce are dependent on landscape composition and configuration. We have touched on several examples here, but there are many more—including seed predation (Tallmon et al. 2003) and seed dispersal (Garcia et al. 2009). And as a reminder that these concepts apply in aquatic ecosystems, fish community assembly can also respond to patch and landscape-level habitat features. Using experimental artificial reefs constructed across a gradient of seagrass cover in the Bahamas, Yeager et al. (2011) found that cover of seagrass at the landscape scale was the most important variable explaining the abundance of benthic fishes and their community structure. Biotic interactions play out in spatially complex landscapes, and this is an active area of research that is likely to yield more and more understanding.

LANDSCAPE ECOLOGY OF SPECIES INVASIONS

Many landscape features may affect a species' ability to disperse, establish, acquire resources, grow, and reproduce; native and nonnative species alike must contend with spatially heterogeneous environments. However, the increased prevalence of nonnative, invasive species in many landscapes and the growing number of landscape-level studies that are concerned with biological invasions prompted us to highlight these issues here. Understanding the distribution and spread of invasive species relates to many of the issues already discussed in this chapter, including the effect of habitat amount and configuration on dispersal and movement, habitat quality on establishment and population growth, and the degree to which the landscape mediates interactions with other species, including the native community. Invasive species have long been an issue of concern in applied ecology (e.g., Elton 1958), and a variety of hypotheses have been proposed to explain invasions (e.g., see review by Hierro et al. 2005). Spatial heterogeneity per se had received little explicit attention (e.g., Melbourne et al. 2007), but studies of landscape influences on nonnative invasive species have increased in recent years.

Kim With raised awareness of "the landscape ecology of invasive spread" in her 2002 paper, which laid out different ways through which landscape structure could affect the spread of invasive species and the invasibility of communities (Fig. 7.16). These included (1) enhancing spread above some threshold level either directly or indirectly via landscape effects on dispersal vectors; (2) affecting stages of the invasion process, such as dispersal or population growth, in different ways; (3) interacting with the distribution of the invasive species to facilitate spread, as through nascent foci; (4) promoting or altering species interactions in ways that enhance invasibility of communities; (5) compromising or enhancing the adaptive potential of native species to resist invasion; and (6) interacting with disturbances in ways that cause resources to fluctuate, which can enhance invasibility. She explored these ideas with a set of simulations using neutral landscape models in which the abundance and configuration of suitable habitat was varied, and this paper laid the groundwork for subsequent studies that explored the role of landscape pattern on different aspects of the invasion process.

Many empirical studies have since documented relationships between landscape heterogeneity and invasion pattern. Some studies have explored species richness of native and nonnative species to determine whether these groups respond differentially to local predictors and landscape context. In the central part of Rocky Mountain National Park, USA, the species richness of native and nonnative plants were positively correlated with several landscape metrics, including edge density, Simpson's diversity index, and interspersion/juxtaposition index, but negatively correlated with mean patch size (Kumar et al. 2006). Analyses were performed at multiple spatial scales, and the best landscape-level models explained 70 % of the variation in nonnative species richness. Inclusion of landscape metrics always improved models of nonnative species richness but explained relatively

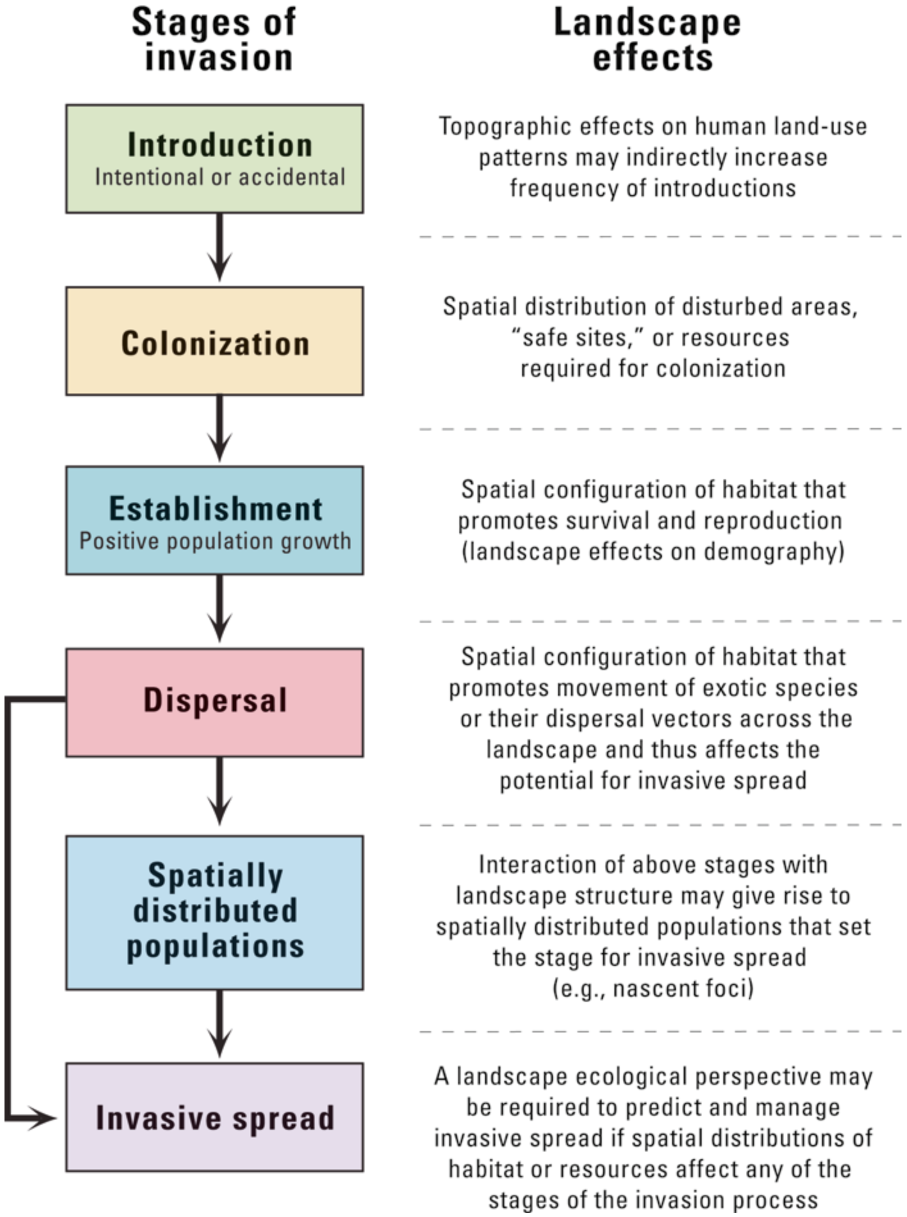


FIGURE 7.16.
Stages of invasion by nonnative species and different ways each stage can be influenced by landscape structure.

ADAPTED FROM WITH (2002)

little variation in native species richness (Kumar et al. 2006). This finding suggested that landscape heterogeneity mattered more for the exotic than for the native plant species in this landscape (Kumar et al. 2006).

Relationships involving landscape predictors and native and nonnative species may change with scale, as illustrated by a study of a nonnative invasive shrub, common buckthorn (*Rhamnus cathartica*), in Minnesota, USA. This shrub species is native to Europe but invasive in North America, where its range and abundance have increased throughout the midwestern USA. In a multiscale study, Knight and Reich (2005) found that the buckthorn cover was negatively related to species richness and cover at fine (1-m) scales. However, the relationship changed with spatial scale: buckthorn cover was positively related to native species cover at the landscape level (Knight and Reich 2005). Species-rich communities have been hypothesized to be more resistant to invasion than species-poor communities, and this was observed at fine scales. However, at broad scales, buckthorn was more likely to occur in landscapes that supported more native species. Another study, which focused on invasion patterns of a nonnative vine, Oriental bittersweet (*Celastrus orbiculatus*), in the Southern Appalachian Mountains, reported different factors predicting presence in areas where the invader was well established and areas where the population was expanding (Albright et al. 2009). These studies again underscore the importance of scale and the potential for relationships to change as scales vary.

Humans can be important facilitators of nonnative species dispersal. Humans move species around both purposefully and accidentally, with land-use altering landscape heterogeneity in ways that increase opportunities for invasion (Kuhman et al. 2011). For example, in the Baraboo Hills of southern Wisconsin, USA, the number of houses in a 1-km buffer around forest plots was strongly and positively associated with the abundance of nonnative invasive plants (Gavier-Pizarro et al. 2010a). In New England, USA, nonnative invasive plant species richness was strongly and positively affected by the area of wildland–urban interface, low-density residential areas, and housing growth (Gavier-Pizarro et al. 2010b). Mechanistically, land-use development can provide suitable habitat for invasives and increase propagule pressure. Land-use history can leave persistent difference in habitat quality that enhance invasibility (Van Holle and Motzkin 2007; Brown and Boutin 2009). In Southern Appalachian forest understories, forest sites that were previously cultivated and abandoned ca. 1905 had more invasives than sites that were not previously cultivated (Kuhman et al. 2010).

Roadsides offer potential habitat and movement conduits for invasive plants, allowing populations in these habitats to serve as local foci for invasive spread into adjacent habitats. In deciduous forests of southeastern Ohio, USA, nonnative species were most abundant along roadsides, and seed-sowing experiments found that roadsides and open areas were better locations for germination and growth of one exotic, *Microstegium vimineum*, than nonroadside sites (Christen and Matlack 2009). Road corridors were also associated with the movement of nonnative plant species into national parks in south-central Chile (Pauchard and Alaback 2004). In a study of seed transport that also differentiated the effect of local vs. distant seed sources, vehicles traveling through tunnels in the vicinity of Berlin, Germany, were found to transport large numbers of seeds and to be responsible for long-distance dispersal events (Von der Lippe and Kowarik 2006).

A key issue in invasive species management at the landscape level is the relative effectiveness of strategies based on offense (containing invaders at their source patches) versus defense (protecting uninvaded destinations from invasion). A modeling study based on the spread of an aquatic invasive species through a network of lakes nicely illustrates this idea (Drury and Rothlisberger 2008). Results showed that offense was better early in invasions, when the goal is to reduce overall spread rates, but defense was better after half the lakes are invaded. When the goal is to protect areas of high conservation value, defensive site protection lowers the per-site rate of introduction. Although developed for lakes, these findings may well apply to other settings (Drury and Rothlisberger 2008). For example, in a study of an ongoing invasion of black cherry (*Prunus serotina*) into forests in Flanders, Belgium, priority control efforts (i.e., offense) were recommended for landscapes with relatively few invaded stands (Verheyen et al. 2007). Spatially explicit predictions of hotspots of invasion under future scenarios offer opportunities to anticipate regional invasion patterns and plan accordingly (e.g., Ibánez et al. 2009). Of particular importance in management of the spread of invasive species is the need to pay attention to interactions of landscape pattern with different aspects of the invasion process (Eschtruth and Battles 2009).

Have general findings emerged from studies of the landscape ecology of species invasions? The relationship between predictor and response variables is clearly scale dependent. Relationships may vary with the type of response variable examined. The presence, abundance, species richness, or spread rate of nonnative species is not controlled by the same drivers—and life-history characteristics of invader and native species must be jointly considered. There is some evidence that habitat configuration may be more strongly associated with the presence or occupancy of invasive species (because it will interact with propagule pressure to influence establishment) but habitat quality may be more associated with the abundance (e.g., cover or biomass) of invasive species (e.g., Predick and Turner 2008). Melbourne et al. (2007) proposed an *environmental heterogeneity hypothesis of invasions*, whereby heterogeneity increases invasion success and reduces the impact to native species in the community, because heterogeneity promotes invasion and coexistence mechanisms that are not possible in homogenous environments. Although invasive species within native habitats are widely regarded as undesirable perturbations, studying the nature of the invasive process and its dependence on landscape pattern provides new insights into these important pattern–process dependencies.

LANDSCAPE GENETICS

A call for integrating landscape ecology and population genetics (Manel et al. 2003) opened up many new opportunities for understanding how geographical and environmental features structure genetic variation within and among populations, and for reconstructing the spatial movements and spread of populations. The term was coined by Manel et al. (2003), who defined *landscape genetics* as an amalgamation of molecular population genetics and landscape ecology that aims to understand the interaction between landscape features and microevolutionary processes, such as gene flow, genetic drift, and selection. Manel et al. (2003) further defined key components to include detection of genetic discontinuities and correlation of these discontinuities with landscape or environmental features. Landscape genetics generally considers *microevolution*, i.e., evolution within a given species, rather than processes that lead to speciation. Landscape genetics is distinct from other areas of genetic inquiry because its approach is spatially explicit and considers how landscape composition, configuration, and matrix quality influence gene flow and spatial genetic variation (Storfer et al. 2007). The appeal of landscape genetics is the potential for investigating a process through genetic data and for analyzing this process in the real world using landscape ecological data (Holderegger and Wagner 2006). Landscape genetics can be an especially valuable tool for understanding functional connectivity and metapopulation structure.

Landscape genetics considers two principal forms of genetic variation. *Neutral genetic variation* refers to variation in genes that have no effect on fitness, that is, they are “neutral,” having no adaptive value, and natural selection does not act on these alleles. Large parts of an organism’s DNA are effectively neutral (Holderegger et al. 2006), and neutral variation is useful in landscape genetics studies to detect spatial relationships among individuals and populations and trace dispersal or movement pathways. Neutral genetic markers are used to estimate gene flow, independent of selective forces, but not to estimate selection. In contrast, *adaptive genetic variation* refers to variability in genes (or quantitative traits) that do affect fitness and are selected by environmental conditions. Thus, studies of selection in heterogeneous landscapes must address adaptive variation. It is rarely possible to directly study the genes responsible for adaptive genetic variation, and researchers often focus on variation in quantitative traits that are of potential adaptive value, such as a plant’s production of chemical defenses to herbivory (Lindroth and St. Clair 2013). To evaluate the adaptive potential of a population or the influence of landscape heterogeneity on fitness, quantitative traits and adaptive variation must be studied.

Early landscape genetics studies examined the effect of putative boundaries (e.g., mountain ranges, rivers, roads) to population movement in landscape, often for a single vertebrate species, and were largely confirmatory (Sork and Waits 2010; Storfer et al. 2010). That is, observers expected populations to be isolated by movement barriers in the landscape, and analyses of genetic structure confirmed that they were. Some studies, however, revealed surprising results. In Yellowstone National Park, USA, rivers were thought to be barrier to movement and gene flow among populations of blotched tiger salamanders (*Ambystoma tigrinum melanostictum*), but genetic analyses revealed that rivers actually facilitated gene flow because recurrent floods mixed the population (Spear et al. 2005). Topographic relief restricts gene flow in many terrestrial species, and drainage structure and currents influence gene flow in many aquatic and marine species (Storfer et al. 2010). Studies have also revealed an influence of *cryptic barriers* to gene flow (i.e., barriers that are not visually conspicuous and may have been unanticipated), such as climate gradients that may relate to a species' environmental limits of tolerance. Genetic studies have confirmed effects of habitat fragmentation on gene flow in some species, most likely because of restricted dispersal among habitat fragments, but other studies have revealed instances where habitat loss and fragmentation did not influence gene flow. For example, gene flow remained high for a mobile, generalist Neotropical seed-dispersing bat, *Artibeus lituratus*, in fragmented Atlantic forest in South America (McCulloch et al. 2013). As with other kinds of landscape legacies, historical landscape patterns may leave a legacy in genetic structure (Keyghobadi et al. 2005).

Some of the unique insights that landscape genetic studies can provide are illustrated by studies linking landscape features with the genetic structure and movement pathways of black bears (*Urus americanus*). Using nondestructive hair-sampling methods, the effects of landscape connectivity on patterns of genetic similarity were assessed among 146 black bears in a 3000-km^2 study region in the mountains of northern Idaho, USA (Cushman et al. 2006). The objective was to understand bear movement patterns and how these were shaped by the landscape. Potential relationships between the bear movement costs and landscape features including land cover, slope, elevation, Euclidian distance, and a putative movement barrier were explored by testing a set of 110 alternative hypotheses (testing alternative hypotheses is a key strength of this analysis). Partial Mantel tests, which measure the degree of associate between two dissimilarity matrices (here, hypothetical least-cost distances and the genetic differences among bears) were used to assess the differential influence of barriers, distance, and landscape features. Genetic structure in the black bear population was primarily related to land cover and elevation; gene flow was facilitated by contiguous forest cover at middle elevations and inhibited by nonforest cover types (Cushman et al. 2006).

A subsequent study then developed a direct linkage between the behavior of individual bears and the genetic structure across the landscape. Using GPS telemetry data, Cushman and Lewis (2010) predicted bear movement paths as a function of elevation, roads, human development, and forest cover. Gene flow is determined by movement during the breeding and dispersal seasons, so the authors hypothesized that movements observed during those seasons would be a function of the same landscape factors identified in the landscape genetic analysis. This hypothesis was supported (Cushman and Lewis 2010). They hypothesized further that landscape resistance maps developed for breeding and dispersal season movements would be highly correlated with the landscape resistance map produced from landscape genetic analysis, but correlations would be weaker for maps produced from movements at other times of year (Cushman and Lewis 2010). Results also supported this hypothesis, showing high similarity between the resistance surface predicted from landscape genetics and that produced by early season movements. The late-season model was very different, with road effects dominating late-season bear movements. The results also suggested that if road density and residential development were concentrated in the elevation zone preferred by bears, the effects on bear population connectivity might be much greater than expected (Cushman and Lewis 2010).

As with many landscape-level studies, among-landscape replication in landscape genetic studies can be difficult. However, the landscape resistance hypotheses for gene flow in black bears were tested in each of 12 different study areas in the north central U.S. Rocky Mountains—thereby providing replication among different landscapes (Short Bull et al. 2011). Among landscape replicates, isolation by landscape resistance was more supported than isolation by distance, but the particular features that influenced gene flow in a given landscape varied. An extremely important implication of this replicated study is that researchers should not automatically conclude that features are unimportant to movement and gene flow of a species if the features are unimportant in a particular landscape (Short Bull et al. 2011).

Landscape genetics is an exciting field that offers much promise for advancing understanding of evolutionary processes in spatially complex landscapes. Landscape genetics has grown exponentially in the past decade concurrent with tremendous advancement in molecular techniques and data analysis tools. The tools and concepts of landscape ecology enable the ecological pressures that influence the genetic structure of populations to be evaluated within the context of large, spatially heterogeneous landscapes (Manel et al. 2003; Guillot et al. 2005; Joost et al. 2007; Storfer et al. 2007; Kozak et al. 2008). Recent studies emphasize the power of landscape genetic approaches for identifying ecological correlates of genetic variation and detecting adaptive genetic variation and trade-offs among different traits (e.g., Manier and Arnold 2006; Kozak et al. 2008; Eckert et al. 2009). Landscape genetics is yielding new insights about the expansion of invasive species, revealing that multiple introductions are common (Handley et al. 2011), and of native species, such as top predators, recovering from earlier extirpation and dispersing in heterogeneous landscapes (Lucchini et al. 2002) or responding to landscape change (e.g., Keyghobadi et al. 1999). Landscape genetics becomes increasingly important as we look forward to rapid changes in the global environment and anticipate how species populations will respond to such change. Understanding evolutionary processes in spatially complex landscapes is critical to understanding the adaptive capacity of populations in spatially heterogeneous and variable environments (Reusch and Wood 2007). Spatial genetic structure results from evolutionary, behavioral, ecological, and stochastic processes operating at different scales, and landscape genetics studies must address scale dependencies (Balkenhol et al. 2009). For greater detail and excellent overviews of landscape genetics, readers are referred to Holderegger and Wagner's review in BIOSCIENCE (Holderegger and Wagner 2008) and the special issue of MOLECULAR ECOLOGY on landscape genetics (Sork and Waits 2010). More integration of landscape ecology and evolutionary ecology could be especially productive.

SUMMARY

Organisms exist in spatially heterogenous environments. Landscape ecologists are particularly interested in how organisms utilize resources that are distributed across a heterogeneous landscape and how organisms live, reproduce, disperse, and interact with each other in space. While studies in population ecology have always been cognizant of spatial issues, wide recognition of the importance of spatial factors affecting population dynamics and community structure became prominent in landscape ecology. Early studies that focused on the diffusion of organisms across homogeneous landscapes were able to predict rates of spread and the number of sites that would be occupied under various conditions. However, it was the development of island biogeography and metapopulation theory that fueled much research on the dynamics of populations in heterogeneous landscapes.

In the late 1980s, interest in Levins' metapopulation model revised and replaced equilibrium island biogeography as a way of thinking about fragmented habitats and heterogeneous terrestrial environments in general. A metapopulation was considered as a collection of subpopulations, each occupying a suitable patch of habitat in a landscape of otherwise unsuitable habitat, forming an interconnected set of subpopulations that function together as a demographic unit. The two key premises in the metapopulation approach are that (1) populations are spatially structured into assemblages of local breeding subpopulations, and (2) migration among subpopulations results in a recolonization following local extinction producing regionally stable metapopulation dynamics. The development of source–sink models resulted when differences between patches were considered. Patches with excess reproduction are source patches, and sink patches occur when local mortality exceeds reproductive success. Source–sink dynamics allow migration of the surplus organisms from the source to the sink patches, maintaining populations in an apparent demographic equilibrium. Landscape ecology adds several features to the consideration of how populations interact with spatial pattern. These include: (1) variation in patch quality, (2) variation in the quality of the surrounding environment, (3) boundary effects, and (4) how the landscape influences connectivity between patches. A main difference between the metapopulation view of nature and that embraced by landscape ecologists revolves around the degree of complexity that is considered.

Many approaches to studying populations in heterogeneous space require identification of suitable and unsuitable habitat. In some instances, this simplification is clear, but in other cases, it is difficult to partition the landscape into "patches" embedded in an unsuitable "matrix." Furthermore, some populations require complementary or supplementary resources from different type of habitat. Landscape and population ecologists have incorporated more continuous representations of habitat suitability or quality into their conceptual frameworks. Many of these approaches use observations of habitat use or occupancy to infer habitat selection, which implies choice among multiple alternatives. Advances in telemetry and analytical methods (e.g., resource selection functions) have produced new ways of assessing habitat patterns and detecting scale-depending effects of landscape pattern on how organisms use their environment. Behavioral landscape ecology seeks to understand the mechanisms that underpin animal distributions and use of heterogeneous landscapes. Movement ecology (Nathan 2008) is a growing research area that may provide an ideal opportunity for improved integration of behavioral ecology and landscape ecology.

There are important concepts relating to scale when the interactions between organisms and spatial pattern are considered because the "appropriate" scales vary among taxa—and among questions. There is a strong imperative to focus on the scales that are appropriate for the organism, recognizing that our human-based perception of scale and pattern may not be the right one. Some differences in appropriate scales are due to various attributes of the organisms, such as differences in body mass. While it is easy to acknowledge that interactions between organisms and spatial heterogeneity must be scale dependent, it is difficult to identify the "right" scales in practice. The concept of ecological neighborhoods offers one practical approach to this thorny issue. Related to the concept of ecological neighborhoods is the notion that organisms may respond to heterogeneity at multiple scales. In addition, the structure of the landscape itself may dictate the scales at which organisms must operate.

The interaction between organisms and landscape pattern can be reciprocal. That is, organisms can both create and respond to landscape pattern. Ecosystem engineers are organisms that physically alter the environment and thus modify, maintain, or create habitat. Foundation species are dominant organisms that provide the physical structure for the rest of the community. The loss of ecosystem engineers or foundation species can trigger large changes in landscape patterns. However, most organism-based studies in landscape ecology have focused on how organisms respond to spatial pattern. There is a vast (and overwhelming) literature on this topic.

A number of insights that have emerged from patch-based studies of organisms and space are presented with examples. These include:

- In general, larger more heterogeneous patches contain more species and often a greater number of individuals than smaller patches of the same habitat.
- The relative abundance of edge and interior habitat affects species diversity within a patch.
- Characteristics of the surrounding landscape (landscape context) can strongly influence local populations within a patch.
- The effect of landscape composition on organisms is often stronger than the effect of landscape configuration.
- Landscape composition strongly influences landscape connectivity.
- Corridors can both add habitat and promote movement.

Spatial considerations may not be needed if habitat is very abundant or if movement is relatively unlimited, and organisms can reach all or most areas of suitable habitat. However, it is important to recognize the limitations of a patch-based view of the world and to know when a more continuous view of spatial heterogeneity is needed.

Research on how species respond to landscape pattern has been extended to consider biotic interactions among species and overall community structure. Predator–prey dynamics have received much attention, with many studies focused on wildlife interactions in seminatural landscapes and on natural enemies of crop pests in agricultural landscapes. Pollination has also been well studied. Many field studies have now demonstrated significant influences (and at multiple scales) of landscape composition and configuration on species interactions. Understanding the spatial setting of species interactions has important implications for conservation and landscape management. At the community level, landscape structure can also influence species turnover and community similarity.

The landscape ecology of invasive spread is another burgeoning topic, and again, many studies now document a strong influence of landscape structure on the presence and pattern of nonnative invasive species. Landscape features can influence a species' ability to disperse, establish, acquire resources, grow, and reproduce; historical land use can also be important. Native and nonnative species alike contend with spatially heterogeneous environments. There is some evidence that habitat configuration may be more strongly associated with the presence of invasive species, and habitat quality may be more strongly associated with the abundance of invasive species.

Landscape genetics has opened up new opportunities for understanding how geographical and environmental features structure populations. Landscape genetics seeds to understand the interaction between landscape features and microevolutionary processes, such as gene flow, genetic drift, and selection. Neutral genetic variation is especially useful for detecting spatial relationships among individuals and populations, but adaptive genetic variation must be studied to evaluate selection in a landscape context. Researchers are beginning to consider the role of spatial heterogeneity by considering spatial selection and spatial inheritance (Schauber et al. 2007). There is much room to explore the links between ecology and evolution in an explicit spatial context, and landscape genetics offers much promise for advancing understanding of evolutionary processes in spatially complex landscapes. Landscape genetics become increasingly important for anticipating species responses to global change.

As ecologists continue to grapple with how organisms respond to spatial pattern, there will be many opportunities for synthesis among population ecology, conservation biology, and landscape ecology.

DISCUSSION QUESTIONS

1. What species attributes determine the spatial and temporal scales needed to characterize the species' abundance and distribution at landscape scales?
2. Habitat connectivity is often measured as a function of the geometry of land cover. Discuss the limitations and uncertainties that these methods based on structural connectivity pose for diverse species groups. How might measures of connectivity be improved?
3. How do corridors promote the persistence of a population within a heterogeneous landscape? When might corridors cause population declines? How are your answers dependent on the spatial scale of analysis?
4. How does landscape heterogeneity influence predator–prey population dynamics and patterns of habitat use? Describe at least three effects and provide examples.
5. How can the effectiveness of corridors for species movement be measured by landscape genetic techniques?
6. What similar scientific principles unite landscape genetics, metapopulation dynamics, and landscape fragmentation studies?

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CHAPTER

8

ECOSYSTEM PROCESSES IN HETEROGENEOUS LANDSCAPES

Understanding the patterns, causes, and consequences of spatial heterogeneity for ecosystem function remains a research frontier in both landscape and ecosystem ecology (Lovett et al. 2005; Chapin et al. 2012). The term, *ecosystem*, was introduced by Tansley (1935) to describe the characteristic and persistent interactions of organisms (plants, animals, and microbes) with their abiotic environment (e.g., water, temperature, radiation) within well-defined landscape boundaries (Likens 1995). Although ecosystems may appear to be discrete (e.g., ponds and watersheds), they do not exist in isolation. Interactions among ecosystems occur as a function of the heterogeneity of the landscape. *Ecosystem ecology* focuses on the flow of energy and matter between organisms and their environment, thus emphasizing pools (i.e., amounts or stocks), fluxes (i.e., rates), and the factors that control pools and fluxes. The spatial dimensions of ecosystem ecology may encompass bounded systems like watersheds, complex landscapes of diverse habitats, or even the biosphere itself; temporally, ecosystem science may cross scales ranging from seconds to millennia (Carpenter and Turner 1998). Ecosystem process rates vary across landscapes at multiple scales, and this variation can be difficult to quantify, explain, and predict. Transfers of matter and energy

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among patches (i.e., losses from donor ecosystems and subsidies to recipient ecosystems) are often important to long-term ecosystem sustainability (Polis and Hurd 1995; Naiman 1996; Carpenter et al. 1999; Chapin et al. 2012).

Ecosystem studies address questions about the capture of light energy by plants, its conversion into organic matter, and its transfer to other organisms; and questions about nutrient cycling, in which essential elements such as phosphorus and nitrogen cycle repeatedly between living and nonliving parts of ecosystems (Golley 1993; Carpenter 1998). From initial descriptions of the structure and function of diverse ecosystems, ecosystem ecology moved toward increasingly sophisticated analyses of function, including food web dynamics, biogeochemistry, regulation of productivity, and structure–function relationships (Golley 1993; Pace and Groffman 1998). Ecosystem ecology cannot be exhaustively reviewed here; interested readers are referred to Frank Golley's history of ecosystem research (1993) and two outstanding ecosystem ecology texts (Chapin et al. 2012; Weathers et al. 2013). From ecosystem studies, ecology has gained an excellent understanding of the mechanisms underlying many processes and how ecosystems develop and change through time. However, understanding patterns, causes, and consequences of spatial heterogeneity in ecosystem function remains a frontier.

When landscape ecologists study ecosystem processes, they often emphasize the causes and consequences of spatial heterogeneity in the rates of ecosystem processes (e.g., net primary productivity or nitrogen mineralization), and how landscape composition and configuration may influence the horizontal movement of materials such as water, nutrients, or sediments. The landscape also provides an ideal template for exploring linkages between organisms and ecosystem processes because the transfer of nutrients within and between ecosystems is often mediated by the actions of organisms (e.g., Jones and Lawton 1995; Seagle 2003; Holtgrieve et al. 2009). In spite of its importance, ecosystem function has received somewhat less attention in landscape ecology relative to other foci, such as disturbance dynamics and organism distributions, but a growing number of studies are now filling this gap.

Why has spatial heterogeneity in ecosystem function remained a research frontier? Determining the patterns, causes, and effects of ecosystem function across landscapes is conceptually young (Jenerette and Wu 2004; Lovett et al. 2005; Massol et al. 2011). In part, this is because of scale complexity; many rates are controlled by microbial dynamics that operate at extremely fine spatial and temporal scales and are difficult to measure (e.g., see discussion of nitrogen mineralization by Schimel and Bennett 2004). It is challenging to work across such a wide range of scales, and process studies are also technically demanding and expensive. Linking microbial mechanisms to landscape patterns of ecosystem processes is particularly difficult (Smithwick 2006). Further, landscape-level estimates of ecosystem function may require integration of multiple types of ecosystem, such as upland forests, wetlands, and lakes (e.g., Burcher et al. 2007; Buffam et al. 2011), which are often studied independently by scientists trained in different disciplines (e.g., freshwater or terrestrial ecology). Nonetheless, understanding ecosystem function in heterogeneous landscapes is important for many aspects of global change, and it offers the potential to enhance linkages between species and ecosystem dynamics for a more complete understanding of landscape function.

CONCEPTUAL FRAMEWORKS: ECOSYSTEM PROCESSES IN HETEROGENEOUS LANDSCAPES

Theoretical Development

Clearly, ecosystem processes are spatially heterogeneous. The basic causes of this variation have been well known for a long time (Jenny 1941); a primary factor driving heterogeneity is the abiotic template, which includes climate, topography, and substrate. In addition, ecosystem processes vary with the species assemblage, disturbance events (including their long-term legacies), and the activities of humans (Chapin et al. 1996; Amundson and Jenny 1997). As with other topics covered in this text, pattern–process interactions are reciprocal. Ecosystem processes affect landscape patterns, as when nutrient mineralization rates influence plant distributions, or patterns of net primary production influence the amount, quality, and location of suitable habitat for an animal population. Landscape patterns also affect ecosystem processes, as when the composition and configuration of land cover in a watershed influence nutrient loadings to wetlands, streams, and lakes, or when the landscape mosaic of habitats affects the redistribution of nutrients by mobile animals. Despite recognizing these reciprocal interactions, ecology has lacked a general theory of ecosystem function that is spatially explicit.

An early conceptual approach for considering interactions among different ecosystem types identified the importance of boundaries—their permeability and/or resistance to the flow of material and energy—on spatial fluxes within complex landscape (Wiens et al. 1985). *Boundaries* were defined as locations where the rates or magnitudes of ecosystem transfers (e.g., energy flow, nitrogen exchange) could change abruptly in relation to those within individual patches (Wiens et al. 1985). Fluxes of materials, energy, and organisms may be driven by resource gradients or by active vectors (e.g., wind, herbivores, etc.) that move materials or energy against existing gradients (Wiens et al. 1985). This seminal paper touched on many themes, including ecosystem–community interactions, which have received considerable subsequent theoretical attention.

The importance of integrating food webs and landscape ecology was recognized by Polis et al. (1997), who observed that subsidies of nutrients and detritus from one habitat to another could increase productivity. This forward-thinking review explicitly recognized the role of landscape variables and boundary features. Polis et al. (1997) noted, "the movement of nutrients, detritus, prey, and consumers among habitats is ubiquitous in diverse biomes and is often a central feature of population, consumer-resource, food web and community dynamics.... The message is clear: Ecosystems are closely bound to one another, be they stream and lake, pelagic and intertidal zones, farms and the sea, forest and river, or ocean and desert."

A conceptual framework based on metapopulation and metacommunity concepts was introduced by Loreau et al. (2003). The *meta-ecosystem* was defined as a set of ecosystems connected by spatial flows of energy, materials, and organisms across ecosystem boundaries. Loreau and colleagues were motivated by the need for a theoretical framework for a spatial ecology that would link community and ecosystem dynamics, and they distinguished a meta-ecosystem from a landscape in several ways. First, they considered that meta-ecosystems need not be continuous and occurring within the same physical, geographic space; in other words, the local ecosystems that comprised a meta-ecosystem could be discrete and distant from each other, as islands surrounded by a sea with which they have few interactions. Second, they argued that a landscape is a physical entity with a characteristic spatial scale, whereas meta-ecosystems can be defined at different scales depending on the organisms, ecosystems, and processes considered. However, landscapes may also be defined across a wide range of scales depending on the processes being considered (see Chap. 1), so this distinction seems artificial. Third, they asserted that a landscape can be studied from a variety of perspectives, including one that is purely descriptive and centered on pattern, whereas the meta-ecosystem concept focused on "the properties of the higher-level, spatially extended dynamic system that emerges from movements at landscape to global scales" (Loreau et al. 2003:675). Again, this distinction seems a bit artificial, although it recognizes that landscape ecology is a broader field. Loreau et al. (2003) then presented a simple meta-ecosystem model of source–sink dynamics among ecosystems, assuming a closed system; results demonstrated strong constraints on local ecosystems because of the spatial coupling among ecosystems. A subsequent body of work has extended these ideas into theoretical frameworks for spatial ecosystem ecology (e.g., Loreau and Holt 2004; Gravel et al. 2010; Massol et al. 2011; Leroux and Loreau 2012). This work is valuable for its ability to apply theory that is well developed in population ecology to material fluxes between ecosystems, although it remains somewhat disconnected from the landscape ecology literature and the large body of empirical work in ecosystem ecology.

A significant theoretical study of spatial linkages between nutrient dynamics and biotic communities was conducted by Jenerette and Wu (2004), who modeled plant–nitrogen interactions. They linked biogeochemistry and plant-community dynamics to assess these interactions on ecosystem function and to understand why nitrogen fixers may be unable to alleviate sustained nitrogen limitation in terrestrial ecosystems. The landscape was represented as a grid, and the spatial model included three layers of data for each grid cell: (1) vegetation type, which could be nitrogen fixers, nonfixers, or unvegetated; (2) nitrogen content, which summed the nitrogen concentration in vegetation and soils; and (3) net primary production, which was determined by the vegetation and nitrogen content. Results demonstrated that these interactions could generate self-organizing spatial patterns, and that the system could regulate productivity and nitrogen content independently of external nitrogen supplies. Importantly, the fine-scale dynamics (cell to cell) could be very different from behavior of the whole, spatially integrated system (Jenerette and Wu 2004).

Increasing recognition of the need to strengthen the conceptual foundation for ecosystem processes in landscapes led to the 10th biennial Cary Conference, organized in 2003 by ecosystem ecologists at the Institute for Ecosystem Studies (Lovett et al. 2005). The central question of this conference was, when do we need to deal with spatial heterogeneity as it affects ecosystem processes, and when can we safely ignore it? Strayer et al. (2003a) had presented a logical approach to answer this question for ecosystem modeling. However, the many different types of entity (e.g., mass, energy, information, organisms) that move simultaneously within and among ecosystems (Reiners and Driese 2001, 2004), and the many different ecosystems juxtaposed in different landscapes, continue to make it difficult to identify general principles.

A Practical Framework

Given these difficulties, it is not surprising the ecologists have approached ecosystem function across heterogeneous landscapes in two general ways (Turner and Chapin 2005) that differ conceptually and practically. One is focused on understanding landscape patterns of biomass and process rates, such as net primary production, decomposition, and nutrient cycling rates. Such studies aim to explain why rates are high in some places and low in others and to predict how these patterns might respond to changing drivers. A second approach emphasizes lateral (i.e., horizontal) fluxes of matter, recognizing that the composition and configuration of the landscape play key roles in mediating these fluxes. Land–water interactions are good examples of such lateral fluxes, and many landscape studies have asked how nutrients derived from land are transported to aquatic systems. Both approaches relate to ecosystem processes in heterogeneous landscapes, but they differ in their relative emphasis on vertical or horizontal fluxes, and practically, they differ in how they are studied.

Thus, two general classes of ecosystem process can be considered (Turner and Chapin 2005). *Point processes* represent rates measured at a particular location

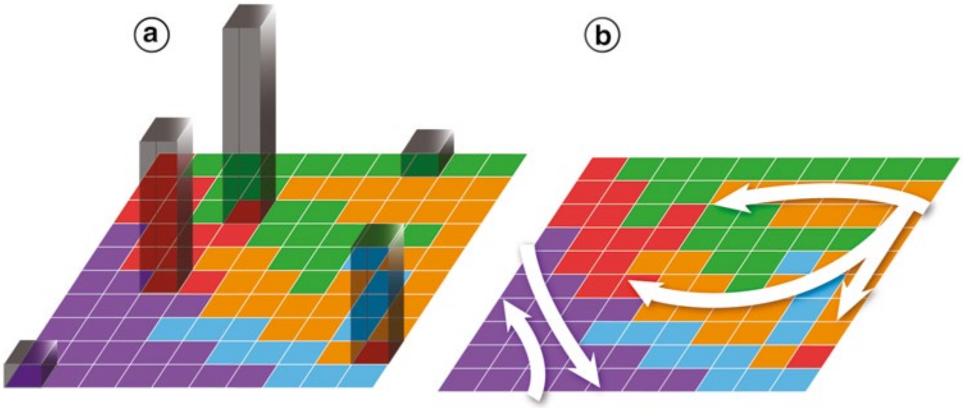


FIGURE 8.1.

Schematic illustration of two general classes of ecosystem processes (**a**) point processes and (**b**) lateral transfers.

ADAPTED FROM TURNER AND CHAPIN (2005).

(Fig. 8.1a), ignoring lateral transfers if they can be assumed to be small relative to the measured response. Examples of point processes include site-specific measurements of net primary production, net ecosystem production, denitrification, or nitrogen mineralization. *Lateral transfers* are flows of materials, energy, or information from one location to another represented in a two-dimensional space (Fig. 8.1b). Examples of lateral transfers include the flow of nitrogen or phosphorus from land to water, or the movements of nutrients across a landscape by herbivores.

Spatial heterogeneity can also be considered from the perspective of the *drivers* of ecosystem processes (biotic and abiotic forces external to the ecosystem) and/or for the ecosystem response variables (e.g., pools or fluxes of materials and energy) altered by changes in ecosystem drivers (Fig. 8.2). Drivers, which vary in space and time, may include soils, topography, climate, and disturbances, which act together to alter pools or fluxes of matter or energy. The combined effect of variation in drivers may be measured by spatial variation in *occurrence* of ecosystem processes, i.e., presence or absence of denitrification (Fig. 8.2a) or spatial variation in the *magnitude* of process rates, i.e., whether denitrification is high or low (Fig. 8.2b, columns). The term, *hot spot*, is often used to identify locations where the magnitude of a flux is especially high (McClain et al. 2003). For lateral transfers, one can also consider the actual pathways of flow (Fig. 8.2b, arrows), much as movement trajectories are tracked for an animal. For both point processes and lateral transfers, an aggregate measure of the function of the heterogeneous system (e.g., average net primary production across the landscape or the total amount of phosphorus delivered from a watershed to a lake) can be assessed. Because many different facets of spatial variation can be considered, it is important to be explicit about the ecosystem process as well as the driver or response for which spatial heterogeneity

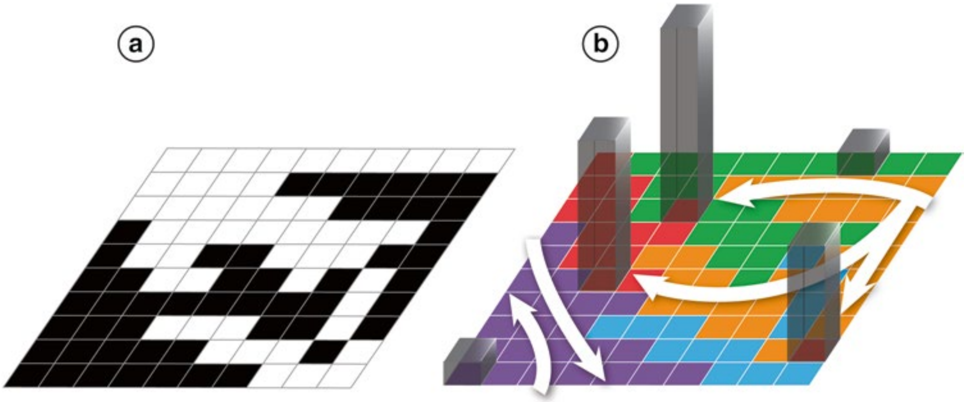


Figure 8.2.

Spatial heterogeneity can be considered in: (**a**) the occurrence of a process, (**b**) the magnitude of the rate or flux (columns), the actual flow paths (arrows) and the template, which is usually multivariate.

Adapted from Turner and Chapin (2005).

is being considered. Using this framework, we next consider a variety of point processes (those related to biomass, carbon cycling, landscape biogeochemistry, landscape limnology) and lateral fluxes (wind-driven transport, land–water interactions, mobile animals) in heterogeneous landscapes.

POINT PROCESSES (VERTICAL FLUXES)

Biomass, Net Primary Production, and Carbon

Early Approaches and Insights

Global and regional variation in *net primary production* (the rate at which organic matter, or carbon, is produced by plants; see Table 8.1 for key terms) on land and in water has long been appreciated by biologists (Leith and Whittaker 1975; Box 1978). Ecologists gained tremendous insights into patterns of biomass and net primary production (NPP) with the advent of remote imagery. Since the first Landsat satellite was launched in 1972, estimation of terrestrial plant production has been an important application of satellite remote sensing (Running 1990). Understanding and predicting such patterns became more urgent as scientists strived to understand the global carbon cycle; tried to quantify carbon sinks, sources, and fluxes; and began to grapple with predicting possible consequences of global warming.

New views of spatiotemporal patterns of vegetation and NPP that were produced in the 1980s by remote sensing scientists caught the attention of ecologists. For example, data from the Advanced Very High Resolution Radiometer (AVHRR)

Table 8.1.
Terms used in studies of carbon cycling and their definitions (based on Chapin et al. 2006 and Hicke et al. 2012a).

Term	Sample units	Definition
Carbon stock or density	g C, g C m^{-2} or Mg C ha^{-1}	Reservoirs of carbon in vegetation and soil pools, including live and dead tree stems, foliage, roots, and soil organic matter
Carbon fluxes	g C m^{-2} year^{-1} or Mg C ha^{-1} year^{-1}	Rates of transfer among carbon pools, including those in the ecosystem and atmosphere
Gross primary production (GPP)	g C m^{-2} year^{-1}	Total amount of atmospheric C fixed by plants
Autotrophic respiration (R_a)	g C m^{-2} year^{-1}	Release of C to the atmosphere by plants
Net primary production (NPP)	g C m^{-2} year^{-1}	GPP – R_a; the net amount of C fixed by plants and available for subsequent use by heterotrophs. Sometimes distinguished by above- or below-ground (ANPP or BNPP, respectively)
Heterotrophic respiration (R_h)	g C m^{-2} year^{-1}	Release of C by microbes through decomposition of organic matter
Net ecosystem production (NEP)	g C m^{-2} year^{-1}	NPP – R_h; the net rate of C accumulated by the ecosystem or lost to the atmosphere. NEP is positive when an ecosystem is a carbon sink and negative when an ecosystem is a carbon source
Net ecosystem exchange (NEE)	g C m^{-2} year^{-1}	Exchange of C between the ecosystem and the atmosphere; NEE is positive when there is a net transfer of C to the atmosphere and may be the same magnitude (but opposite in sign) as NEP
Net biome production (NBP)	g C m^{-2} year^{-1}	Rate of flux of C to and from ecosystems; NBP includes NEP as well as losses of C through such processes as combustion and leaching (e.g., of dissolved inorganic or organic carbon)

Carbon stock or density represents an amount; all other terms below are rates and thus require time.

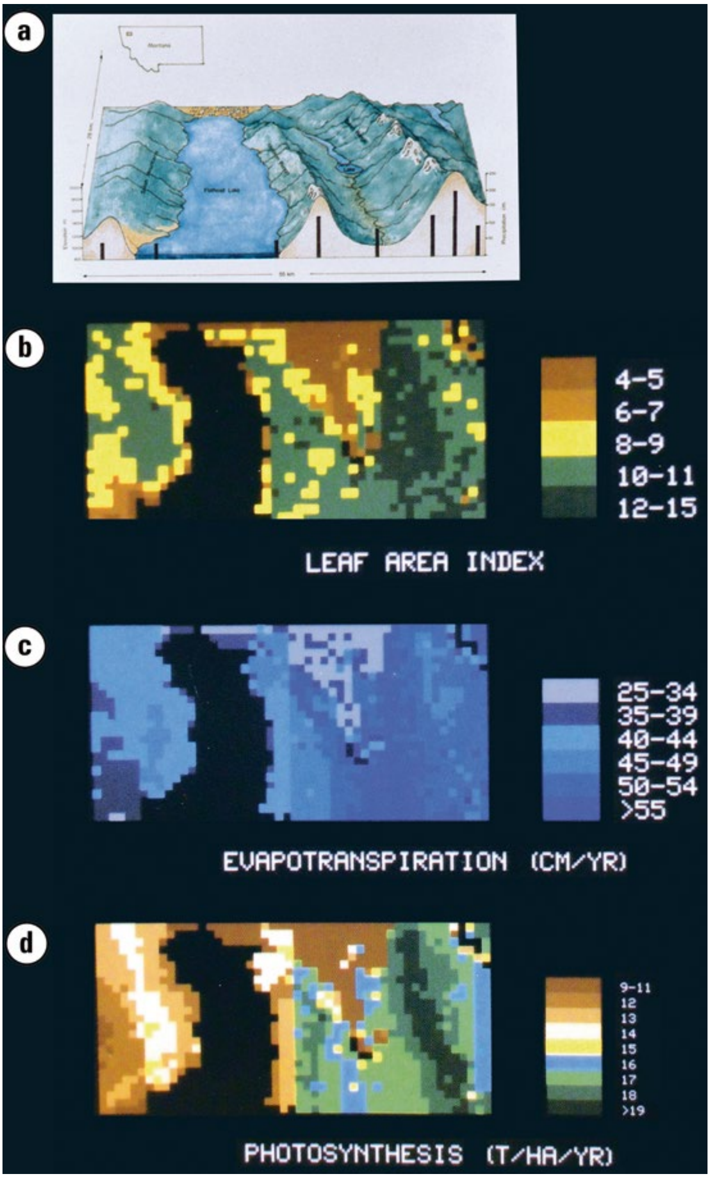
satellite, which provided daily images of the earth at a resolution of 1.1 km, were used to generate vegetation maps for Africa (Tucker et al. 1985), North America (Goward et al. 1985), and the globe (Justice et al. 1985). These maps relied on the dimensionless *normalized difference vegetation index* (*NDVI*), a ratio of the difference between near-infrared (NIR, 0.725–1.1 m) and red (RED, 0.58–0.68 m) portions of the spectrum: NDVI = (NIR – RED)/(NIR + RED). The value of the NDVI is directly related to the presence of photosynthesizing vegetation, providing an indirect measure for mapping vegetation status and growth (Jensen 1996). NDVI has proven to be quite useful, as it relates well to *leaf area index* (*LAI*) (Sellers 1985, 1987) and, in turn, to NPP (Goward et al. 1987). LAI—the ratio of leaf area to ground area, usually reported as m^2/m^2—is a useful index for a variety of ecosystem processes, including the interception of light and water by the vegetation, attenuation of light through the canopy, transpiration, photosynthesis, and nitrogen content. Ecologists estimating ecosystem processes across landscapes routinely measure LAI, in part because it can be well estimated for large areas by satellite imagery (Running 1990).

Vegetation indices derived from satellite data offered new ways of exploring spatial variation in ecosystem structure and function at broad scales. For example, Riera et al. (1998) hypothesized that variability in vegetation cover and biomass should be related to topographic relief and to land use/land cover at the spatial extent of full Landsat Thematic Mapper (TM) images (~185 km swath). The *simple ratio vegetation index* (*SR*) [defined as the ratio between TM3 (the reflectance in band 3, 0.63–0.69 m, corresponding to the red portion of the spectrum), and TM4 (the reflectance in band 4, 0.76–0.90 m, the near-infrared) of the Landsat TM sensor] and the NDVI were compared across 13 study sites representing a wide range of biomes in North America. Marked differences in landscape heterogeneity were observed among the landscapes. Desert and grassland landscapes had low mean NDVI and low overall heterogeneity, whereas forested landscapes had high mean NDVI but also low overall heterogeneity. Spatial heterogeneity was greatest for those landscapes that had intermediate values of the vegetation indices (Riera et al. 1998).

Ecologists began combining remote imagery and other spatial data with ecosystem simulation models to predict spatiotemporal patterns of NPP in the late 1980s. Early advances were driven by the need to link global models, such as the general circulation models (GCMs) used to simulate the global climate, with changes in vegetation. Running et al. (1989) were among the first to integrate biophysical data obtained from many sources and use these data to execute an ecosystem model over a large landscape. They used a 28- × 55-km coniferous forest landscape in western Montana, USA, and built a simple GIS in which climate and soil data were stored. The model required an LAI estimate for each grid cell, and this estimate was obtained from satellite imagery. In addition, the model required soil water-holding capacity for each grid cell and daily meteorological data. The ecosystem model FOREST-BGC (Running and Coughlan 1988) was then run in each of the 1200 grid cells representing the landscape to predict spatial patterns of annual evapotranspiration and net photosynthesis. The resulting estimates of LAI, evapotranspiration, and photosynthesis (Fig. 8.3) demonstrated the power of these new integrative methods for producing spatially explicit projections of variation in ecosystem processes and offered insights into interactions among the controls on these processes (Running et al. 1989).

Extensive empirical studies were also conducted during the 1980s and 1990s on regional patterns of primary production, the accumulation of soil organic matter, and

Figure 8.3.
(**a**) Schematic diagram showing prominent physiographic features of a 1540-km^2 study area in western Montana in which Running et al. (1989) combined satellite imagery, GIS, and an ecosystem simulation model to predict patterns of ecosystem processes. Maps of (**b**) leaf area index (LAI), (**c**) annual evapotranspiration, and (**d**) annual net photosynthesis for the 28 × 55 km study area using 1.1-km grid cells. LAI was estimated by satellite, microclimate data were extrapolated from a model, and ecosystem processes were simulated with the FOREST-BGC model. From Running et al. (1989) and reproduced with permission from the Ecological Society of America.



biogeochemical cycling; studies from the Great Plains region of North America nicely illustrate this approach. Using an extensive data set containing measurements of aboveground net primary production (ANPP) from 9500 sites throughout the Central Grassland region of the United States, Sala et al. (1988) evaluated (1) the spatial and temporal pattern of annual production for the region and (2) the importance of climatic variables as determinants of the pattern of ANPP when the site-level data were aggregated to major land resource areas. Results demonstrated that general trends in processes like net primary productivity and decomposition could be predicted reasonably well by broad-scale variability in temperature, precipitation, and soils (Sala et al. 1988). The analyses by Sala et al. (1988) confirmed the importance of water availability as a control on ANPP, with the regional spatial pattern of production reflecting the east–west gradient in annual precipitation. ANPP was lower in the drier western part of the region and higher in the more moist eastern areas, but the spatial pattern shifted eastward during dry years and westward during wet years (Fig. 8.4). The analyses revealed an interaction between precipitation and soil-water holding capacity. When annual precipitation was <370 mm, sandy soils with low soil-water holding capacity were predicted to be more productive than loamy soils with high water-holding capacity. The opposite pattern was predicted when precipitation was >370 mm. This occurs because bare-soil evaporation is lower in sandy soils than in loamy soils because water penetrates more deeply into the soil; runoff is also lower in the sandy soils. Sala et al. (1988) also observed from their empirical analysis that a model will need to include a larger number of variables to account for the spatial pattern of the same process as the scale of analysis becomes finer. The pattern of the process at the coarse scale constrained the pattern at the finer scale; thus, variability at the finer scale will be accounted for by factors at that scale plus the factors that determine the pattern at the coarse scale. Temporal relationships between precipitation and ANPP in arid regions also show promise for mapping changes in shrub canopy cover and other ecological state changes characterized by shifts in plant functional types and/or ANPP (Williamson et al. 2012).

Many landscape studies of biomass and productivity now integrate data from multiple sources, including forest inventories, intensive plot measurements, and remote sensing (e.g., Van Tuyl et al. 2005; Zhang et al. 2007), in an attempt to understand ANPP and carbon fluxes at regional scales. For example, landscape studies have become increasingly important for understanding how carbon storage and fluxes vary with climate warming. Using Landsat imagery and high-resolution repeat aerial photography, Fraser et al. (2014) found evidence that the "greening" of the western Canadian arctic between 1985 and 2011 was driven by increased temperature. This greening was driven by increased cover of erect dwarf and tall shrubs and decreased cover of lichens. A 4 °C increase in winter temperature over the past 30 years was associated with warmer soils and enhanced nutrient mineralization rates and explained this vegetation change. However, multiple drivers were important; local increases in shrub growth were also attributable to disturbances caused by wildfire, exploratory gas wells, and drained lakes (Fraser et al. 2014).

Spatially extensive field measurements of biomass or ANPP may be combined with statistical models to explain variability and extrapolate patterns to the landscape. For example, in the western portion of the Greater Yellowstone Ecosystem, aboveground net primary production (ANPP) was sampled in 90 forest stands stratified by forest type, stand age, and elevation class (Hansen et al. 2000). Forest type and elevation explained 89 % of the variation in ANPP. The landscape

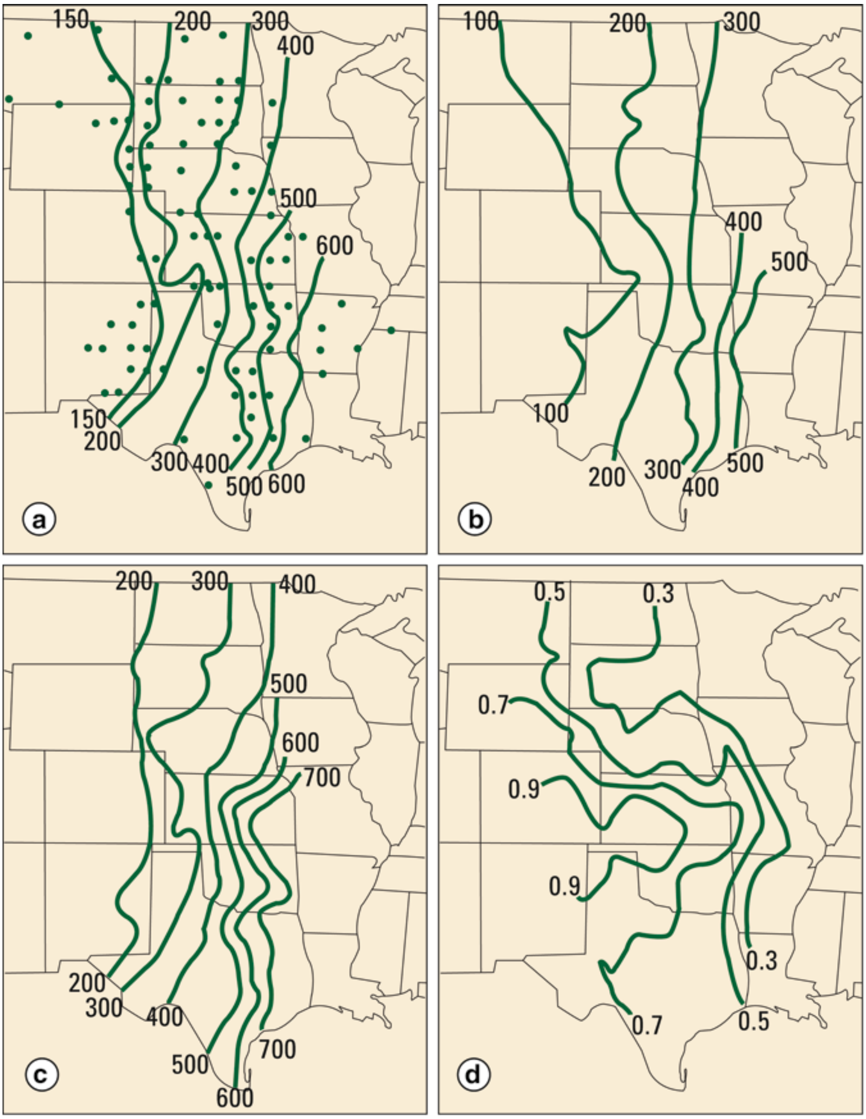


Figure 8.4.

Isopleths of aboveground net primary production (ANPP, g/m^2) for the Central Grassland region of the USA (**a**) during years of average precipitation, (**b**) during relatively dry years, (**c**) during relatively wet years. (**d**) Isopleths show the relative variability in production between favorable and unfavorable years, estimated as: (ANPP$_{wet}$ – ANPP$_{dry}$)/ANPP$_{average}$.

Adapted from Sala et al. (1988).

extrapolation revealed that most (72 %) of the landscape was relatively low in ANPP, but hotspots of ANPP (>4.5 Mg ha^{-1} year^{-1}) occupied about 6 % of the study landscape (Fig. 8.5a). In another study in Yellowstone, areas that burned in the 1988 Yellowstone Fires were sampled in 1999 to determine how ANPP varied

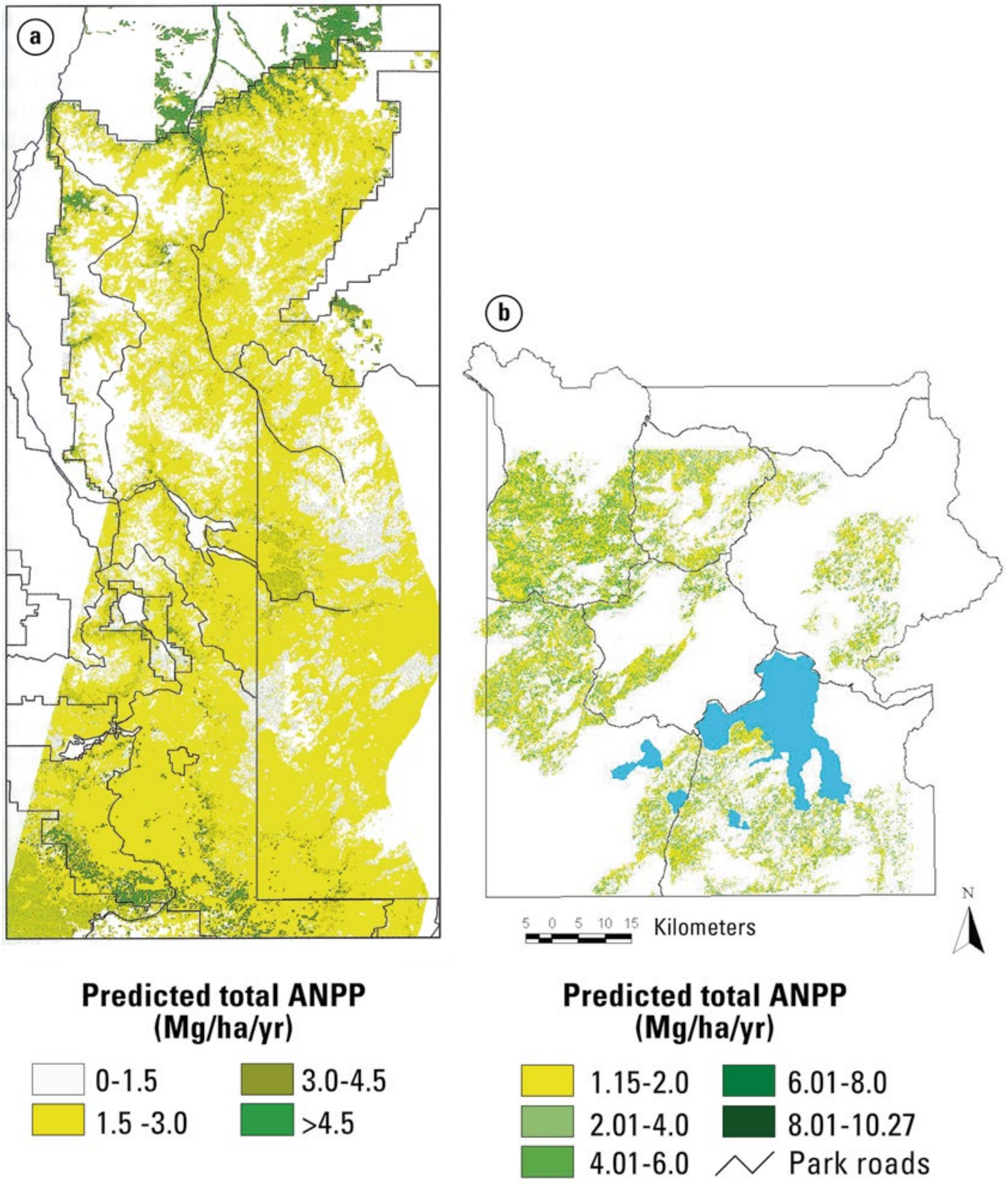


Figure 8.5.

Landscape maps of aboveground net primary production (ANPP) in (**a**) the western portion of Greater Yellowstone in forests of different type and age, and (**b**) in young postfire forested areas of Yellowstone National Park that burned in the 1988 Yellowstone Fires.

Adapted from Hansen et al. (2000) and Turner et al. (2004b).

across the landscape in young postfire stands of the same age (Turner et al. 2004b). This study found a fine-grained mosaic of variability in ANPP in the 10-year-old forests (Fig. 8.5b); about 68 % of the burned landscape had relatively low ANPP (<2.0 Mg ha^{-1} $year^{-1}$), but areas of high ANPP (>4 Mg ha^{-1} $year^{-1}$) occupied 10 % of the burned landscape. The spatial variability in this essential ecosystem process rate was striking, given that these were young forests of the same age, and strongly related to landscape patterns of tree density, which was a legacy of the fire (see Chap. 6).

Landscape Heterogeneity and Regional Carbon Dynamics

Understanding the influence of landscape heterogeneity for regional estimates of carbon cycling is an important area of research. Studies of how primary productivity and carbon fluxes are responding to rapid recent warming in the Arctic provide a nice example of the need to understand landscape patterns of driving variables. Permafrost structures much of the boreal landscape and exerts strong control on carbon fluxes (e.g., Turetsky 2004). Future carbon stores in high-latitude ecosystems will depend on the mosaic of permafrost persistence and thaw across the landscape because processes like photosynthesis and respiration are enhanced by permafrost thaw (Belshe et al. 2012). To assist with upscaling of ecosystem process measurements in tundra, Lee et al. (2011) characterized the spatial heterogeneity of carbon fluxes created by permafrost thaw and *thermokarst* development (i.e., the irregular surface of marshy areas and small hummocks that forms as permafrost thaws). Using replicated sampling grids, they found relationships between carbon flux measurements (annual gross primary production, annual respiration, and annual net ecosystem exchange) and surface subsidence, soil thaw depth, and aboveground biomass, along with spatial structure in all variables. This information informed a model for predicting carbon exchange of the entire landscape and within particular patches (Belshe et al. 2012). Such studies also highlight the danger of quantifying regional carbon fluxes in heterogeneous landscapes from single flux-tower sites because vegetation and topoedaphic conditions may drive variability in fluxes (Emanuel et al. 2011; Sturtevant and Oechel 2013). Even in urban settings, carbon fluxes depend on the surrounding land-use matrix (Groffman et al. 2006a). Carbon fluxes can and do vary with landscape context; incorporating landscape variability into regional estimates of biomass, productivity, and carbon flux remains an important research challenge.

As drivers of landscape pattern and change, disturbance and recovery are fundamentally linked to regional carbon balance and must be considered in regional carbon studies (Bradford et al. 2008; Kurz et al. 2008; Flannigan et al. 2009). Disturbances release carbon stored in biomass to the atmosphere, either quickly, as with combustion during a fire, or over decades, as trees killed by insects, disease, or drought decompose. Forests again become carbon sinks as the vegetation recovers from disturbance, and net losses and gains of carbon over a region may balance over long time periods. For example, much of the carbon lost during fire is regained once a stand has recovered (e.g., Kashian et al. 2006; Campbell et al. 2012), with little net effect on atmospheric carbon over the fire cycle. In subalpine conifer forests of western North America, carbon is usually recovered in about 100 years (Bradford et al. 2008; Smithwick et al. 2009). Moreover, significant amounts of stable carbon (e.g., charcoal) remain in the ecosystem following fire and can persist for centuries, suggesting that wildland fires could be a significant long-term sink for some carbon that would otherwise cycle back to the atmosphere (DeLuca and Aplet 2008). Soil charcoal plays other roles, as well, such as stimulating nitrification, which can enhance growth of vegetation following fire (DeLuca et al. 2006). Because fire regimes are changing in many places, understanding effects of increased fire frequency, size, and severity on net carbon storage is of importance. If fires reoccur before carbon stocks have recovered, a forest that used to store carbon over the long term may switch from a sink to a source (Kashian et al. 2006; Smithwick et al. 2009). For example, a short-interval fire in Alaska eliminated the accumulated dead wood biomass in a black spruce forest and substantially reduced forest carbon storage (Brown and Johnstone 2011). Understanding how future fire regimes may affect landscape carbon dynamics is an important research priority.

Biotic disturbances like forest pathogens and insect outbreaks also affect carbon cycling, and Hicke et al. (2012a) provide an excellent review of disease-induced changes in carbon stocks and fluxes. Forest primary productivity is reduced immediately following insect or pathogen attack, and repeated growth reductions can lead to tree mortality. However, in the years following the attack, primary productivity can increase rapidly because growth of surviving vegetation is enhanced (Hicke et al. 2012a). Across landscapes, there is great uncertainty about net effects on carbon cycling because consequences depend on the type of pest or pathogen, the severity of the outbreak or attack (such as the amount of tree mortality), time since disturbance, and spatial extent of the disturbed area. Progress in understanding how carbon stocks and fluxes vary over space and time and how they respond to disturbances is sorely needed.

Landscape ecologists also recognized that primary production changes with land-use change. For example, annual net primary production in the Georgia, USA, landscape increased from 2.5 to 6.4 Mg ha^{-1} between 1935 and 1982 (Turner 1987b). These changes were associated with widespread abandonment of croplands followed by natural succession to pine and increased urbanization in some areas. Low NPP through the 1960s reflected persistent effects of poor agricultural practices, which had caused fertility of the land to decline (Turner 1987b). The importance of spatial and temporal variation in NPP for regional and global patterns of carbon dynamics has also been recognized. Secondary forests in regions that experienced widespread cropland abandonment could serve as important terrestrial sinks for global carbon (Delcourt and Harris 1980), although ongoing land-use changes may counter this effect. Levy et al. (2004) simulated global carbon balance between 1770 and 1990 with and without land-use change. In the absence of land-use change, terrestrial carbon storage was predicted to increase by 145 Pg carbon. However, when land-use change was represented, the terrestrial system became a net source of 97 Pg carbon. Thus, land use shifted the terrestrial system from a sink to a source of carbon (Levy et al. 2004). Understanding how future climate and land use will interact to influence carbon balance is of high priority.

Estimates of regional carbon storage and fluxes should account for the entire mosaic of different ecosystem types within a region, but this is not always done. In regional studies, terrestrial ecologists often consider only the terrestrial ecosystems, aquatic ecologists focus on the surface waters, and wetlands may be few and ignored by both groups. However, these ecosystems process and store carbon differently, and the whole suite of systems must be considered to understand the function of intact landscapes. One study that integrated aquatic and terrestrial components to generate a complete regional carbon budget was done for the 6400 km^2 Northern Highlands Lake District of northern Wisconsin (Buffam et al. 2011). Estimates of carbon stocks and fluxes were obtained from field surveys, tower-based CO_2 flux measurements, modeling, and published literature. Results found that landscape C storage was dominated by peat-containing wetlands and lake sediments, which covered only 20 % and 13 % of the landscape, respectively, but stored >80 % of the total carbon on the landscape. The largest regional carbon flux, however, was an accumulation of carbon into aggrading forests that were still recovering from nineteenth and twentieth century harvest, but C fluxes into wetlands and from surface waters were still of consequence (Buffam et al. 2011). Carbon pools and fluxes were spatially heterogeneous but showed strikingly different landscape patterns, as locations of greatest C density are not necessarily the locations where annual fluxes are greatest (Fig. 8.6), underscoring the need to consider both stocks and flux rates when studying landscape C cycling.

The potential role of landscape configuration in regional carbon studies is intriguing. Productivity and carbon fluxes are often predicted at points (or grid cells) because the vertical flux is usually dominant. However, several studies have reported interesting effects when landscape pattern and patch characteristics are considered. It is commonly assumed that carbon dynamics can be measured or modeled within homogenous patches, then summed to predict over broader scales, but Smithwick et al. (2003) found that might not always be the case. Edge-induced variation in light levels, wind exposure, and tree mortality in fragmented forest landscapes lead to errors in the additive approach (Smithwick et al. 2003). Similarly, Robinson et al. (2009) used field data and Biome-BGC to demonstrate that within-patch and landscape heterogeneity, as well as habitat fragmentation, had a strong effect of forest carbon cycling and storage. Vitousek et al. (2009), using advances in remote sensing, found that fine-scale patterns of topography affected community structure and N concentration levels as a consequence of human disturbance and the recent

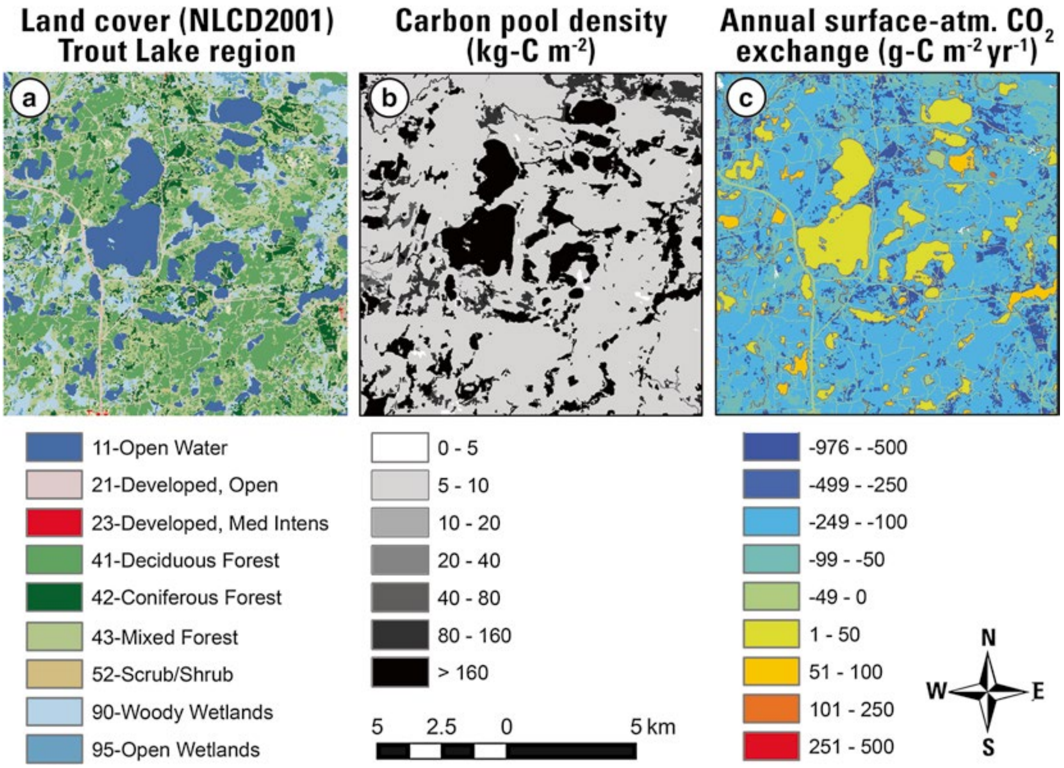


FIGURE 8.6.

Map of spatial variation in carbon pools and fluxes for an 18 × 18 km region of the Northern Highlands Lake District in northern Wisconsin, USA. (**a**) Land cover. (**b**) Pool sizes of carbon. (**c**) Average annual surface-atmosphere fluxes of carbon.

ADAPTED FROM BUFFAM ET AL. (2011).

introduction of invasive plants. Together these results show that point-specific studies can identify key ecosystem processes, but additional studies are required to understand the often-unexpected effects of landscape heterogeneity.

Landscape Biogeochemistry

Interest in obtaining broad-scale estimates of other biogeochemical process rates and their spatial variability increased with the emergence of landscape ecology, in part because of human intrusions into global nutrient cycles, which often make more of a given element available in a biologically active form (Mooney et al. 1987; Groffman et al. 1992; Vitousek et al. 1997b). Nitrogen (N) is a useful indicator of ecosystem function for several reasons. Nitrogen often limits primary productivity in temperate ecosystems (Vitousek and Howarth 1991; Reich et al. 1997), and the presence of nitrate in soil water and streamwater can be used as an indicator of disturbances that lead to N leaching (Bormann and Likens 1979; Vitousek and

Melillo 1979; Parsons et al. 1994). Nitrogen influences the quality of water and air, and anthropogenic modifications of the global N cycle have profound effects on the form and function of terrestrial and aquatic ecosystems (Vitousek et al. 1997b). The unprecedented production of industrially fixed N has resulted in massive global inputs of N that have resulted in N no longer limiting NPP in many ecosystems. As with carbon, N dynamics are affected by abiotic gradients and biotic interactions. For example, temperature and soil type explained a considerable amount of variation in both N mineralization rates and ANPP in cool temperate forests (Reich et al. 1997). *Nitrogen mineralization* (the production of ammonium by aerobic soil bacteria) and *nitrification* (conversion of ammonium to nitrate by aerobic soil bacteria) produce the inorganic forms of nitrogen available for plant uptake.

Spatially explicit studies of biogeochemistry were few in early landscape studies, but they quickly increased in number and began to provide insights into scale-dependent relationships between ecosystem pattern and process. For instance, Morris and Boerner (1998) quantified nitrogen mineralization and nitrification potentials in soils of hardwood forests in southern Ohio at three spatial scales: (1) the regional scale, represented by four study areas of 90–120 ha separated by 3–65 km; (2) the local scale, represented by three contiguous watersheds within each study area; and (3) the topographic scale, represented by different landscape positions within each watershed. Their results underscored the importance of understanding the patterns of variation manifested at different spatial scales. They observed no effect of spatial scale for nitrification potential in their study area, suggesting extrapolation from plot to region should be relatively easy. However, this was not the case for nitrogen mineralization potential or storage of organic carbon, which varied significantly with topographic position making this variable an important element of any extrapolation from plots to regions. Studies in other locations have confirmed the importance of topographic effects on soil nitrogen dynamics.

A regional study in southern Michigan, USA, used soil texture and natural drainage class to extrapolate rates of denitrification obtained from a landscape study (Groffman and Tiedje 1989) to an even larger area using a GIS (Groffman et al. 1992). *Denitrification* is the production of gaseous nitrogen from nitrate by soil bacteria in the absence of oxygen and is a critical process for reducing nitrate pollution in groundwater. Results from Groffman et al. (1992) revealed that spatial patterns of soil texture strongly influenced regional patterns of denitrification. Loam-textured soils occurred under 47 % of the forests in the region but accounted for 73 % of the denitrification. Sandy soils occurred under 44 % of the regional forest but produced only 5 % of the regional denitrification, and clay loam soils, which underlie 9 % of the regional forest, produced 22 % of the denitrification (Groffman et al. 1992).

Since these early studies, numerous researchers have attempted to quantify and explain spatial variability in pool size or cycling rates of different elements, and these studies span a wide range of spatial scales. Ecologists have made substantial progress in quantifying landscape patterns of process rates, but the spatial heterogeneity of the multiple factors responsible for such patterns is challenging to study and poorly understood (Turner and Chapin 2005). Nutrient pools and fluxes are influenced by multiple drivers that may differ in importance and/or interact across a wide range of scales (e.g., Reich and Oleksyn 2009). Landscape ecologists have assessed spatial dependence in nutrient pools and fluxes over a wide range of scales, from within single stands (e.g., Smithwick et al. 2005; Turner et al. 2011) to large regions (e.g., Vasquez et al. 2012).

In addition to local habitat and soil conditions, landscape configuration may influence some biogeochemical process rates. In an experimentally fragmented landscape in Kansas (USA), laboratory measurements of N-related fluxes in soils obtained from forest patches of different size revealed interesting differences attributed to patch size (Billings and Gaydess 2008). Rates of net N mineralization and gross nitrification were substantially greater in soils collected from small vs. large patches. The differences were associated with greater root biomass and root N concentration in the small patches compared to the large patches (Billings and Gaydess 2008). Results suggested that N cycling may differ in small vs. large patches, and furthermore, that gaseous losses of N from the ecosystem may relate to forest patch size (Billings and Gaydess 2008). Given the extent of habitat fragmentation worldwide, these intriguing results bear testing in other landscapes to determine how general patch size-related differences in nutrient cycling may be and to understand the causal pathways involved.

In landscapes that have a strong imprint of human activity, land-use legacies influence biomass, productivity, and nutrient pools and fluxes. Thus, landscape history matters when interpreting contemporary ecosystem process rates. In secondary forests that developed after agriculture was abandoned, soil organic matter can be substantially reduced. For example, soils in secondary forests of central New York (USA) had 15 % less organic matter and 16 % less carbon in the top 10 cm of soil than adjacent primary forest (Flinn and Marks 2007). Stand history also influences the mass, C, and N in downed coarse wood (Currie and Nadelhoffer 2002). Land-use effects are not only observed in forests. In an agricultural watershed in southern Wisconsin (USA), soil phosphorus concentrations varied with land use and showed spatial scale dependence (Bennett et al. 2005). Fertilizer applications and pasturing increased mean soil P and variance in soil P and shifted the spatial scale of variation to larger extents, and these alterations persisted through time (Bennett et al. 2005). As discussed in Chap. 2, historical agriculture can homogenize fine-scale variation in soils, thereby changing the spatial scale of variability in nutrient pools and fluxes.

Recent studies have demonstrated an important role of species interactions in structuring spatial patterns of soil nutrients and foliar nitrogen. Species interactions play out spatially on landscapes, creating opportunities to influence heterogeneity of process rates. For example, wolves can modulate landscape patterns of nutrients by configuring the distribution of ungulate carcasses (Bump et al. 2009a). Using a 50-year record that included >3600 moose carcasses from Isle Royale National Park, Michigan (USA), Bump et al. (2009a) found elevated soil nutrients, microbial biomass, and foliar nitrogen at kill sites for at least 2–3 years (Fig. 8.7). The locations of wolf-killed moose deposition varied in space and time with wolf hunting behavior, but the activities of this top predator structured the patterns of important ecosystem processes in the landscape (Bump et al. 2009a) and changed competitive dynamics between herbs and trees (Bump et al. 2009b). These and other studies of how trophic dynamics and carcasses can influence landscape patterns of ecosystem processes in soils and vegetation (e.g., Danell et al. 2002) are providing exciting new insights about ecosystem function in heterogeneous landscapes.

Identifying spatially and temporally explicit nutrient cycling rates remains challenging because the processes and the drivers vary so much in both space and time. Consider *denitrification*, a key process that removes excess nitrate from ecosystems, returning reactive nitrogen to the stable pool of nitrogen in the atmosphere. Denitrification is often highest in wetlands and inundated floodplains. However, denitrification is difficult to measure and model, in part because small areas (*hotspots*) and brief time periods (*hot moments*) can account for a high percentage of the denitrification activity that occurs in a landscape. The process is relatively well understood, but mapping and modeling spatial hotspots in the environment are difficult; it is challenging to predict the spatial pattern of drivers, such as nitrate availability and carbon substrate, along with the timing and location of the anoxic conditions required for the process. Many scientists and land managers are interested in predicting this microbial process at the landscape level because the effects of nitrate on soils, water quality, and air chemistry are substantial. Predicting rates and patterns of *methanogenesis* (anaerobic production of methane, a potent greenhouse gas) presents similar challenges. In addition, the technical training and high cost of labor and the laboratory analyses required to assess nutrient cycling in space and time can be prohibitive for many researchers.

With new sensors and rapid methodological advances, remote sensing data offer tremendous promise for scaling field measurements to the landscape and detecting evidence of nutrient limitation on net primary productivity over large areas. The biophysical and biochemical characteristics of canopy foliage are important indicators of forest ecosystem patterns and processes. Spectroscopy has long been used to develop linkages between narrow-band indices and leaf-level physiology for nondestructive measurements of foliar properties such as structure (e.g. leaf thickness), biochemistry (i.e., chlorophylls and accessory pigments, nitrogen), and water content (e.g., Carter 1998; Gao and Goetz 1994; Knapp and Carter 1998). Satellite-based spectrometers can now make many of these measurements remotely with high spectral resolution. Imaging spectroscopy (i.e., hyperspectral imagery) can be used to assess forest ecosystem function (Asner and Martin 2008) and to infer soil

FIGURE 8.7.
Illustration of how predator–prey dynamics in Yellowstone National Park, USA, are associated with spatial heterogeneity in ecosystem function. The hunting behavior of wolves influences the spatial and temporal distribution of carcasses on the landscape. *Top* and *center* photos show wolf-killed elk carcass sites in spring. Decomposing carcasses release nutrients that enhance tissue quality in grasses (*bottom*), which creates preferred grazing patches at carcass sites.
PHOTOS BY JOSEPH K. BUMP.

processes from canopy spectral reflectance (Martin and Aber 1997; Wessman et al. 1989, 1998; Ollinger et al. 2002; Ollinger and Smith 2005). For example, prediction of foliar nitrogen using hyperspectral imagery is now well established (Smith et al. 2003; Townsend et al. 2003). Continued advances in measurement technology in the future will likely open new avenues for understanding landscape patterns of nutrient stocks and fluxes.

Landscape Limnology

Spatial variability is also observed among the aquatic systems embedded in landscapes. Limnologists have long considered lakes as discrete units of study, owing in part to the natural boundary of the lake shoreline (Forbes 1887). Understanding the spatial patterns within individual lakes (e.g., patterns and processes in stratified lakes) occupied early limnologists (Forel 1892; Birge and Juday 1911; Soranno et al. 1999). Recognition of the interactions between lakes and their watershed and airshed lead to a broader view of lake ecosystems in which atmospheric inputs and catchment characteristics such as geology, land use/land cover, and topography were recognized as important influences on the chemical and trophic status of lakes (Likens 1985). Lake ecologists began to recognize spatial variation among lakes at landscape scales (Kratz et al. 1997), and the importance of the regional spatial scale for explaining variation among lakes (Cheruvelil et al. 2013). We focus here on aggregate measures of individual lakes and how lakes vary from one another, then consider land–water interactions in the next section in the chapter.

Landscape limnology refers to the spatially explicit study of lakes, streams, and wetlands and the effects of these spatial patterns on ecosystem processes across temporal and spatial scales (Soranno et al. 2010). The core principles of landscape ecology provide the foundation for landscape limnology, building on earlier arguments that landscape ecology can be usefully applied to aquatic ecosystems (e.g., Stanford 1998; Wiens 2002). Landscape limnology treats the freshwater landscape as embedded in a terrestrial and human mosaic and considers a variety of landscape ecological variables as they apply to freshwater ecosystems: (1) patch characteristics, (2) patch context, (3) patch connectivity and directionality, and (4) spatial scale and hierarchy (Soranno et al. 2010).

Some landscapes are dominated by presence of many lakes that cover a substantial proportion of the land surface (e.g., northern Sweden; northern Minnesota and Wisconsin in the US). The glacial processes that created these landscapes result in lakes that generally lie within the same geologic setting, experience the same weather, and, therefore, might be expected to be similar in their biological and chemical properties. However, lakes within such a *lake district* (regions of similar geomorphology and climate that contain many lakes) often show remarkable differences from one another, even though they are in close proximity. The many factors that can contribute to differences between lakes include lake size and depth, internal processes such as nutrient cycling and/or trophic dynamics, and the characteristics of the surrounding landscape.

A lake's *landscape position* can be measured by its hydrologic position in the regional flow system that connects adjacent lakes within a given landscape (Kratz et al. 1997) (Fig. 8.8). Many hydrologic properties of a given lake will be determined directly by landscape position. In northern Wisconsin, groundwater is an important component of the water balance of lakes; some lakes have no inflow of surface water. The amount of groundwater that enters a lake is directly influenced by the position of the lake in the landscape. Lakes higher in the flow system (which may differ in elevation by only a few meters in northern Wisconsin) have different relative sources of water than lakes lower in the flow system (Webster et al. 1996). Precipitation comprises a greater proportion of the water input to lakes higher in the landscape than to the lower lakes, which receive a greater proportion of their water input from groundwater. Groundwater typically has greater ionic strength than precipitation because of its contact with the soils and substrate; thus landscape position influences ionic concentrations in lakes (Fig. 8.9).

Soranno et al. (1999) analyzed long-term data from nine *lake chains* (lakes in a series, connected through surface or groundwater flow) from seven lake districts of diverse hydrogeomorphic setting in North America. The study asked: (1) are there predictable spatial patterns in chemical, algal, and water quality variables along lake chains, and (2) do lakes that are closer together in a chain behave more similarly through time? Results indicated that spatial and temporal patterns of lakes

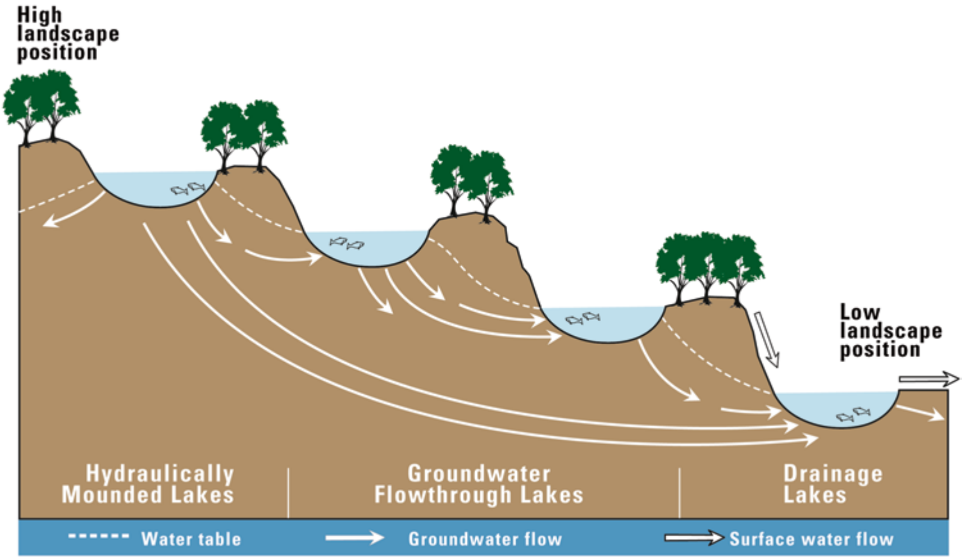


FIGURE 8.8.

Illustration of the concept of landscape position applied to lakes.

MODIFIED FROM WEBSTER ET AL. (1996).

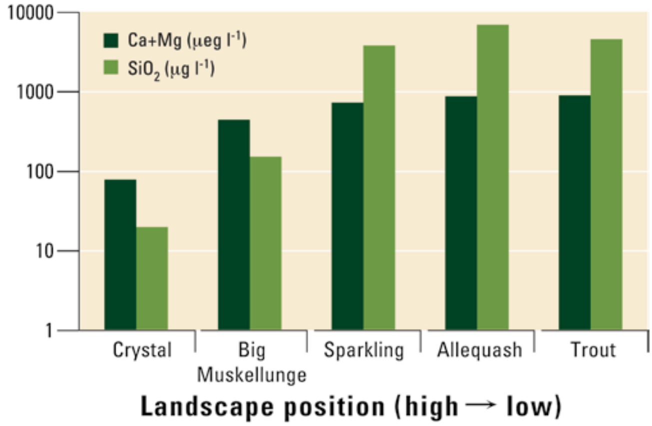


FIGURE 8.9.

The relationship between landscape position and the calcium plus magnesium and dissolved reactive silica concentrations in the five clearwater lakes of the North Temperate Long-term Ecological Research site in northern Wisconsin, USA. These five lakes lie within the same groundwater flow system. Crystal Lake is highest (i.e., headwater) and Trout Lake is lowest in the flow system.

ADAPTED FROM KRATZ ET AL. (1997).

within a lake district were organized along gradients of geology (depth of glacial till and spatial heterogeneity in soil characteristics), hydrology (water residence time and whether lakes were dominated by surface or groundwater flow), and some measure of landscape influence (e.g., ratio of watershed area to lake area). The spatial patterns along lake chains for a wide range of variables were surprisingly similar across lake districts. For example, weathering variables, alkalinity, conductivity, and calcium generally increased along lake chains, but these patterns were weaker in regions situated in calcium-rich tills or having high local heterogeneity in geologic substrate. Concentrations of particulate nutrients and measures of algal biomass increased along lake chains in drainage lakes, but not in the groundwater-dominated lakes. Regarding temporal patterns, landscape position was important in determining **synchrony** (a measure of the degree to which lake pairs within a lake district behave similarly through time [Magnuson et al. 1990]) between lake pairs only for variables related to weathering. For most variables, synchronous behavior in lakes within a lake chain was unrelated to lake spatial position.

Landscape processes that influence the amount of dissolved organic carbon (DOC) entering a lake can affect the magnitude and vertical distribution of primary production within the lake. Lakes with high concentrations of DOC tend to be tea colored, and the brown color reduces the clarity of the water and hence the light penetration. Colored DOC is derived mainly from the soils or wetlands rich in organic matter within the landscape surrounding a lake. Therefore, the position of the lake relative to sources of allochthonous (i.e., from external sources) DOC inputs can be a dominant factor determining net primary productivity within the lake (Kratz et al. 1997; Gergel et al. 1999). Interestingly, many existing lake data sets emphasize large lakes, which are often important for the human populations in a given region, but this may bias regional estimates of lake properties. In the Northern Highlands Lake District of northern Wisconsin, Hanson et al. (2007) selected a random sample of 168 lakes that spanned the full size distribution of lakes and measured a broad suite of limnological variables in each lake. The results demonstrated that most lakes were small (median lake area was 1.1 ha), although half of the surface area of water was in relatively few large lakes. Small lakes had high concentrations of DOC and lower concentrations of dissolved inorganic carbon compared to large lakes. Including small lakes in the lake survey resulted in a median DOC concentration that was about 50 % higher than it would have been without the smaller lakes (Hanson et al. 2007). Thus, all lakes need to be included in regional estimates of lake carbon; excluding small lakes will introduce bias.

Results from these studies suggest that a landscape perspective for lakes is informative and robust. This perspective argues that lakes are not isolated ecosystems but rather are embedded in a landscape matrix, with lakes interacting with one another and with the terrestrial environment. Soranno et al. (1999) argued further for an expansion of this view to encompass the set of lakes, streams, and wetlands that occur within a landscape; these aquatic systems are often treated separately (and as independent entities), yet they are often connected spatially and functionally. A landscape perspective fosters such integration, which is among the goals of landscape limnology (Soranno et al. 2010).

Studies of how lakes vary and change are also being aided by the increased availability of remotely sensed data. Indices derived from satellite data provide insights into patterns and trends in lake water clarity, which can be strongly related to lake trophic status. Landsat imagery has been used to map water clarity lakes in Wisconsin (Chipman et al. 2004), Minnesota (Olmanson et al. 2008), Maine (McCullough et al. 2012), and New Zealand (Hicks et al. 2013), although relatively few studies have yet explored the regional drivers of such patterns (Soranno et al. 2010). Understanding the drivers of interannual and among-lake variation in water clarity in lake-rich landscapes remains a key challenge in landscape limnology (Soranno et al. 2010).

LATERAL FLUXES (HORIZONTAL TRANSPORT)

Several common *vectors* (factors that facilitate transport of matter and energy across landscapes against existing gradients) often dominate ecosystem processes (see Reiners and Driese 2004 for in-depth discussion). For instance, wind (aeolian) and water (fluvial) effectively move organic matter, soils, and nutrients across many landscapes. Soluble nutrients are often moved by gravity-driven fluvial transport, and nutrients adsorbed to soils are translocated by erosion and colluvial transport. Animal locomotion is also important for moving matter and nutrients from one place to another. Within heterogeneous landscapes, nutrient pools and fluxes vary spatially, and landscape composition and configuration may affect lateral fluxes. Most examples of lateral transfers involve the transmission of matter (Reiners and Driese 2004). Here, we use three examples to illustrate these principles.

Redistribution of Litter and Organic Matter

Nutrient fluxes via litter redistribution can be extensive in some landscapes. For example, redistribution of leaf litter in a topographically and edaphically complex landscape on the Allegheny Plateau in Ohio was substantial, with some landscape positions (ridgetops and upper slopes) serving as a net source of litter, and others (side and lower slopes) serving as a net sink (Boerner and Kooser 1989). Litter movements from one cover type may even provide enough nutrients to subsidize productivity in another. Over a 3-year period in an agroforestry landscape in Guangdong Province, southeastern China, about 11 % of the litterfall in an *Acacia mangium* plantation was transported to a *Dimocarpus longan* orchard (Shen et al. 2011). The influx of windblown litter accounted for 9–59 % of the total nutrient inputs in the orchard, depending on the element. Thus, the transfer of nutrients could potentially enhance fruit production in the orchard.

Nutrient redistribution from croplands to remnant patches of natural vegetation in agricultural landscapes may lead to nutrient overenrichment in the remnants (Duncan et al. 2008). In areas of grain production in Australia, soils are nutrient poor and formerly supported semiarid woodland. Conversion to agricultural land uses was accompanied by crop fertilization and manure associated with sheep farming. Nutrients accumulated in remnant patches, but the effect varied with patch size and configuration. Small (<3 ha) patches of remnant vegetation were nutrient accumulation zones, as were the edges of large patches, especially on the windward sides of the patches (Duncan et al. 2008). Results were consistent with two different transport mechanisms. Enrichment in small remnants resulted from livestock sheltering, and enrichment in large remnants was due to wind and water movement of nutrients in soil and litter.

In lake ecosystems, airborne fluxes of nutrients represent additional important transfers of matter between ecosystems (Vander Zanden and Gratton 2011). Lakes occupy lower spots on the landscape and often receive gravity-driven inputs of matter, organisms, and nutrients. The influx of *terrestrial particulate organic carbon* (*TPOC*), such as windblown leaf litter, twigs, pollen, or insects derived from surrounding terrestrial ecosystems, can be important sources of organic matter that support lake metabolism. Many lakes are net heterotrophic systems, meaning that they require carbon inputs from outside the system (e.g., Hanson et al. 2003). The relative importance of such allochthonous inputs is greater for smaller lakes, which have higher perimeter:area ratios, than for larger lakes (Vander Zanden and Gratton 2011). Most leaf litterfall inputs occur within 10 m of the shoreline (France and Peters 1995), suggesting there will be strong effects of lake size and shape on litter inputs (Vander Zanden and Gratton 2011).

Long-range transport of soil, smoke, and dust particles from one ecosystem to another—sometimes from one continent to another—has long been recognized as a significant process capable also of transporting important nutrients around the globe (e. g., Perry et al. 1997; Prospero 1999). Dust plumes that originate in Africa are often visible in remote imagery and provide significant inputs to the landscapes of southeastern USA (Prospero 1999). Intercontinental transfers have been identified as important nutrient inputs to a variety of ecosystems.

Nutrient Loading to Aquatic Ecosystems

Land–water interactions are perhaps the best studied examples of lateral fluxes of nutrients across landscapes because problems associated with *eutrophication* (excess nutrients) are so widespread in aquatic ecosystems. A common theme underlying many studies of land–water interactions is the degree to which land uses in the uplands, and the spatial arrangement of these land uses, influence water quality (Strayer et al. 2003b). Freshwater and estuarine ecosystems act as integrators and centers of organization within the landscape, touching nearly all aspects of the natural environment and human culture (Naiman et al. 1995; Naiman 1996; Boynton et al. 1995; Correll et al. 1992). Noel Hynes, widely regarded as the father of modern stream ecology, stated, "We must not divorce the stream from its valley in our thoughts at any time. If we do, we lose touch with reality" (Hynes 1975). Land–water interactions are apparent even in relatively undisturbed landscapes. For example, studies along a toposequence of tundra, sedge, and shrub communities along a slope in Alaska revealed the importance of ecosystem adjacencies to nutrient transformation and movement (Shaver et al. 1991). The entire sequence of community types occurred along a few hundred meters, but large differences were observed in the rates of plant uptake, mineralization, and transport between ecosystems.

Improving understanding of the complex relationships between the land and water is an important goal of basic and applied research in landscape ecology. Freshwaters are degraded by increasing inputs of silt, nutrients, and pollutants from agriculture, forest harvest, and cities (Carpenter et al. 1995, 1998). Consider a watershed containing croplands or pastures. Farmers often apply fertilizers high in nitrogen and phosphorus (P) to their fields, but not all of the added N and P is taken up by the plants. When it rains, some of these nutrients are leached from the soil and transported through the watershed and into the stream by both surface and subsurface water flow. Like agricultural areas, cities and suburbs are important contributors to such "*nonpoint source*" *pollution*—that is, pollution that does not come from a single source, like a pipe, but rather is delivered from widespread areas of the landscape. Homeowners often apply as much fertilizer and pesticides per unit area to their lawns as farmers do to their crop fields, and a portion of these nutrients end up in nearby aquatic systems. Lakes and reservoirs fill more rapidly with mud from agricultural and urban land uses, and the growth of nuisance plants including toxic blue-green algae is promoted by the increased silt and nutrients. Regional changes in land use cause widespread eutrophication of many lakes on the landscape. Eutrophication also makes lakes more similar to one another, because the lakes are all dominated by species that can tolerate eutrophic conditions. Therefore, the diversity of lake types within a landscape is reduced as all lakes become eutrophic and converge to have similar species (Carpenter et al. 1995).

The nutrients most often considered in studies of land–water interactions are nitrogen and phosphorus. Economic and health concerns about excess nitrogen inputs into aquatic ecosystems are growing throughout the world (e.g., Cole et al. 1993; Mueller and Helsel 1996; Vitousek et al. 1997a, b). In rivers, nitrogen biogeochemistry is sensitive to land-use patterns, the structure of the riparian zone, and river flow regimes (Cirmo and McDonnell 1997). Coastal "*dead zones*," such as the extensive zone of hypoxia that develops each year in the Gulf of Mexico (Rabalais et al. 2002; Dodds 2006), result from excess inputs of nitrogen, mostly derived from anthropogenic activities in the watershed. Accumulation of excess phosphorus in lakes has long been recognized as a driver of eutrophication, and again, this is largely derived from human land use (e.g., Carpenter et al. 1998; Wagner et al. 2011).

Understanding the effects of land-use patterns on water quality and the spatial scales over which these effects are manifest has been an important goal of landscape ecological studies since the mid-1980s. For example, Osborne and Wiley (1988) analyzed the nitrogen and phosphorus concentration of streams in the Salt River Basin, Illinois, and used regression analysis to determine whether there was a relationship to land-use patterns mapped from aerial photos. Results demonstrated that the amount of urban land cover and its distance from the stream were the most important variables in predicting nutrient concentrations in the streamwater. Numerous studies have found significant relationships between land use and concentrations of nutrients in lakes and streams (Strayer et al. 2003b).

The impacts of human activities on sediment and nutrient budgets of watersheds are well documented (Carpenter et al. 1998). Historically, broad-scale forest clearing and conversion to agriculture or residential land use has led to increased erosion and transport of sediments and nutrients into estuaries and the lower portions of river systems. In the Chesapeake Bay basin (USA), such impacts have been documented for postsettlement times (1700s—present) both broadly for the entire Bay (e.g., Brush 1984, 1986, 1989, 1997) and specifically for selected tributaries (e.g., Jordan et al. 1997a, b). An extensive analysis of land-cover effects on stream ecosystems revealed that land cover was significantly correlated with numerous aquatic response variables, including annual nitrate flux (Strayer et al. 2003b). In a study of 210 lakes in Denmark, Nielsen et al. (2012) found that the proportion of agricultural land use in the entire watershed was best in explaining variation in lake water quality, suggesting that transport mechanisms within entire catchments are important for nutrient export to lakes. However, the spatial scale that is best for predicting ecological responses varies among response variables (Strayer et al. 2003b); predictive power declined in small watersheds, suggesting that the spatial arrangement of land-cover patches may be critical at these smaller scales.

Landscape patterns are also important for water quality in urban areas, as illustrated for Minneapolis-St. Paul by Detenbeck et al. (1993). In 33 lake watersheds in the Minneapolis-St. Paul area, landscape and vegetation patterns were obtained from aerial photographs and then compared with measured lake water quality. When lakes were embedded in a forest-dominated watershed, they were less eutrophic and had lower levels of chloride and lead. In contrast, lakes with substantial agriculture in their watersheds were more eutrophic; percent urban land use in the watershed was also positively correlated with lake phosphorus (Detenbeck et al. 1993). Wetlands were also important; when wetlands remained intact in the watersheds, less lead was present in the lake water. Along an urban to rural gradient in the Chesapeake Bay watershed, phosphorus exports were low in small, forest-dominated watersheds with low-density residential land use, and greatest in the lower watershed that was dominated by urban land use (Duan et al. 2012).

The increasing number of studies of land–water interactions that consider urban land uses also has led to a greater emphasis on the role of impervious surfaces. With increasing area devoted to roads, parking lots, and buildings, the ability of water to percolate through the soil is impeded. This decrease in perviousness of the catchment leads to a decrease in infiltration and an increase in surface runoff (Paul and Meyer 2001). As the percentage of impervious cover increases to 10–20 %, runoff doubles; with 35–50 % impervious cover, runoff triples (Paul and Meyer 2001). Understanding ecosystem processes in urban landscapes remains a topic of keen interest, as models developed in unmanaged or agricultural systems do not translate well to the urban setting (Kaye et al. 2006). Human influences such as impervious surfaces, engineered water-flow paths, landscaping choices, and irrigation all have important influences on urban biogeochemistry and land–water interactions (Kaye et al. 2006; Pickett et al. 2008).

Problems associated with nonpoint pollution have stimulated a variety of modeling studies designed to relate runoff and nutrient loading in aquatic systems to upland dynamics. In an early modeling study examining spatial variability in the loss, gain, and storage of total nitrogen, Kesner and Meentemeyer (1989) combined a simple mass-balance model with a GIS database to study N dynamics in an 11,490-ha agricultural watershed in southern Georgia, USA. Results demonstrated that it was possible to quantify and map source and sink regions of N in a watershed and that the riparian zone was critically important in buffering this watershed against excessive losses of N.

A simple model of phosphorus transformation and transport for the Lake Mendota watershed, Wisconsin, provided useful insights into the effects of land use on water quality (Soranno et al. 1996). The watershed of Lake Mendota is dominated by agricultural and urban land uses, and the lake itself has a long history of limnological study (Brock 1985; Kitchell 1992). Soranno et al. (1996) developed a GIS-based model of phosphorus loading in which phosphorus-export coefficients varied among land uses. Phosphorus is usually bound to sediments, and phosphorus delivery to the lake is attenuated by the terrestrial landscape. Soranno et al. (1996) accounted for this by weighting the contribution of phosphorus to the lake by a given grid cell by its distance from the lake. Because of the network of storm sewers serving the urban areas of Madison, Wisconsin and surrounding communities, urban areas were treated as though they were adjacent to streams. The model was then used to compare phosphorus loadings in Lake Mendota under current patterns of land use, presettlement land use, and projected future land use in which the urban area increased nearly twofold. Because rainfall events drive runoff, simulations were conducted for both high- and low-precipitation years. Results demonstrated that most of the watershed did not contribute phosphorus loading to the lake; most P came from a relatively small proportion of the watershed, ranging from 17 % of the watershed contributing during low-precipitation years to 50 % during high-precipitation years. A sixfold increase in phosphorus loading was estimated to have occurred since settlement. Results also demonstrated the importance of riparian vegetation in attenuating phosphorus runoff (Soranno et al. 1996). Ongoing research in this well-studied lake continues to yield new insights about how changes in land use and land cover influence lake hydrology, nutrient loading, and eutrophication (Carpenter et al. 2007).

Riparian corridors, including wetlands and floodplain forests, are conspicuous elements of many landscapes and important mediators of land–water interactions (Naiman and DeCamps 1997). Freshwaters are especially sensitive to changes in these adjacent lands. *Riparian buffers*—areas of relatively undisturbed vegetation along streams or adjacent to lakes—generally slow the transport of nutrients and sediments from upland agricultural–urban areas to adjacent aquatic ecosystems. Because riparian vegetation and associated microbial communities can take up large amounts of water, sediment, and nutrients from surface and groundwater draining agricultural areas within a catchment, they act as temporary storage areas that substantially reduce net discharges of nutrients into aquatic ecosystems. Disturbances to riparian zones can quickly release stored nutrients and sediments making the structure and dynamics of these landscape units an important component of management and restoration of streams in developed landscapes (Bernhardt and Palmer 2007; Craig et al. 2008; Kaushal et al. 2008).

Wetlands, floodplains, and riparian vegetation zones have been extensively altered by agricultural and urban development (Turner et al. 1998a) (Fig. 8.10).

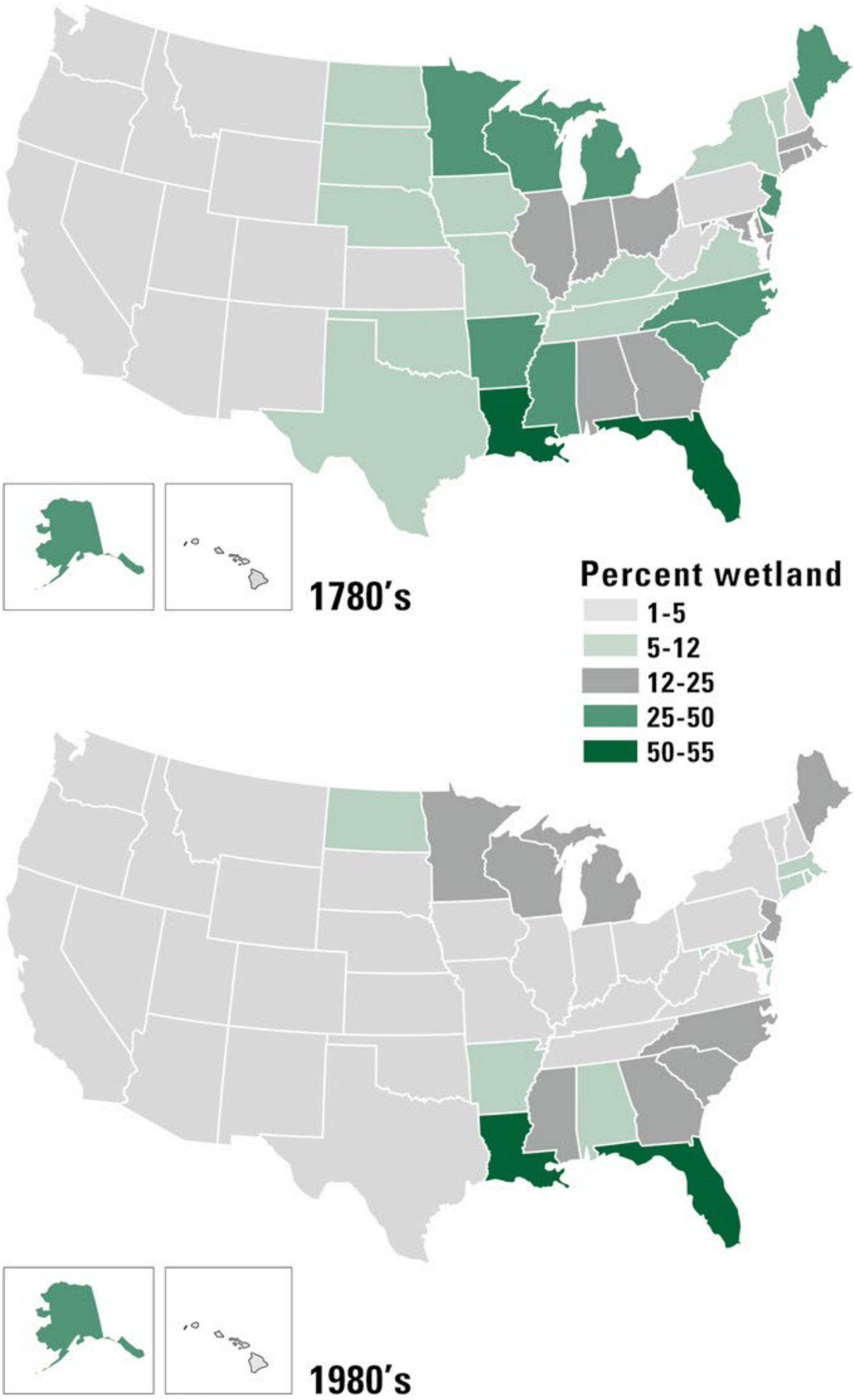


FIGURE 8.10.

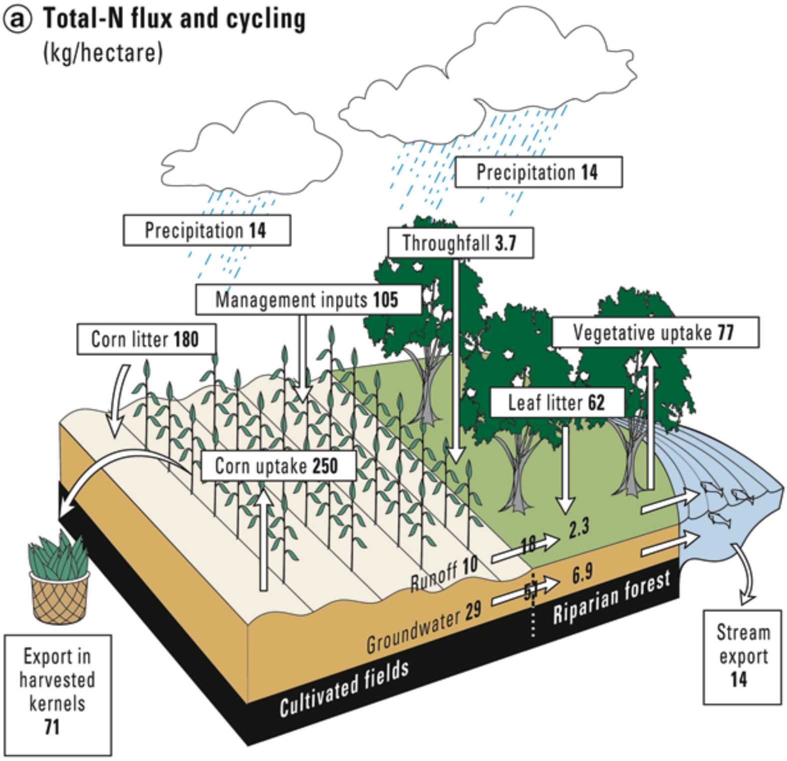
Wetland losses from the United States.

ADAPTED FROM TURNER ET AL. (1998A).

Woody riparian vegetation once covered an estimated 30–40 million ha in the contiguous United States (Swift 1974). At least two-thirds of that area has been converted to nonforest land uses, and only 10–14 million ha remained in the early 1970s. Floodplain clearing for agriculture, urbanization, and water resource development has been responsible for much of the loss of riparian forests. Since the 1970s, the total amount of forest and natural vegetation in riparian buffers has remained similar, declining by <1 % (Jones et al. 2010). A classic example of the loss of riparian forest has been described for the Willamette River, Oregon (Sedell and Froggatt 1984). Prior to 1850, the streamside forest extended up to 3 km on either side of a river characterized by multiple channels, sloughs, and backwaters. By 1967, government-sponsored programs for forest clearing, snag removal, and channelization (channel deepening and straightening) reduced the Willamette River to a single uniform channel that had lost over 80 % of its forest and land–water edge habitats. For an excellent review of the function of riparian zones, interested readers are referred to Naiman and DeCamps (1997).

In the mid-Atlantic region of the United States, studies of nutrient dynamics in mixed agricultural watersheds have nicely demonstrated the nutrient-removal function of riparian vegetation. Substantial quantities of particulate materials, organic nitrogen, ammonium-N, nitrate-N, and particulate phosphorus were removed in an agricultural watershed when waters flowing from a corn field passed across approximately 50 m of riparian forest (Peterjohn and Correll 1984) (Fig. 8.11). The effectiveness of vegetated riparian buffer strips (forest and grass) in retaining nutrients moving from adjacent agricultural lands was also examined by Osborne and Kovacic (1993). Results demonstrated that nitrogen runoff was reduced by 90 % for both forest and grassy riparian buffers, but that forest vegetation retained more nitrogen whereas grassy vegetation retained more phosphorus. This process of nutrient removal is ecologically important because it can substantially reduce cultural eutrophication. Thus, the presence and location of particular vegetation types can strongly affect the movements of materials across the landscape and help to regulate the quality of surface waters within the landscape.

The spatial pattern of riparian vegetation—i.e., variation in length, width, and gaps—influences its effectiveness as a nutrient sink. Weller et al. (1998) developed and analyzed models predicting landscape discharge based on material release by an uphill source area, the spatial distribution of riparian buffer along a stream, and retention of material within the buffer (Fig. 8.12). The buffer was modeled as a grid of cells, with each cell transmitting a fixed fraction of the material received. Variability in the riparian buffer width reduced total buffer retention and increased the width needed to meet a management goal (Weller et al. 1998). Variable-width buffers were less efficient than uniform-width buffers because transport through gaps dominated discharge, especially when buffers were narrow; average buffer width was the best predictor of landscape discharge for unretentive buffers, while the frequency of gaps was best for narrow, retentive buffers (Weller et al. 1998).



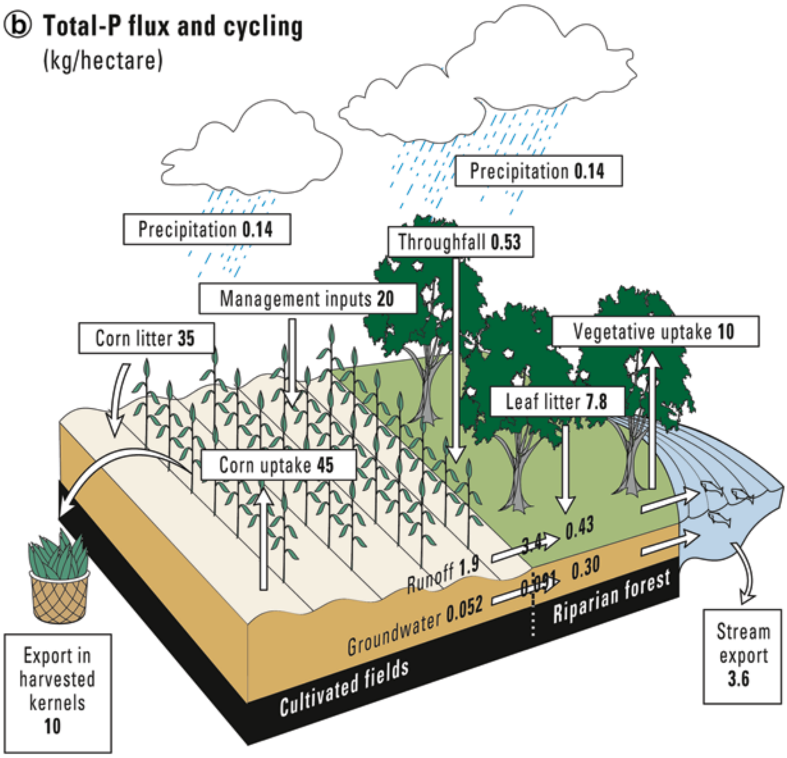


Figure 8.11.

Diagram of total-N flux and cycling (**a**) and total-P flux and cycling (**b**) in a study watershed from March 1981 to March 1982. All values are kg/ha of the respective habitats.

Adapted from Peterjohn and Correll (1984).

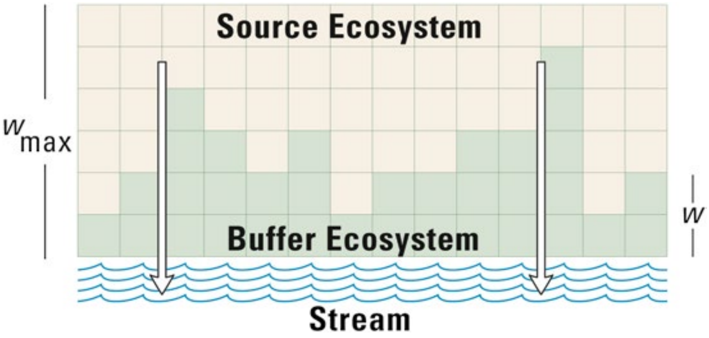


FIGURE 8.12.
Conceptual model of a landscape with a riparian buffer. The landscape is divided into a grid, and cells along the stream are occupied by the buffer ecosystem. Water and materials flow downhill from the source ecosystem, through the buffer, and to the stream. Weller et al. (1998) developed models in which the width (w) and length of the riparian buffer were varied, along with the width (w_{max}) of the entire simulated landscape, to evaluate the effectiveness of the buffer at retaining nutrients.

ADAPTED FROM WELLER ET AL. (1998).

This heuristic model offered predictions that were amenable for testing in a variety of riparian systems.

Riparian zones have a significant effect on water quality, but the spatial extent of that effect remains unclear (Fig. 8.13). That is, is it only the riparian zone that is important in maintaining water quality, or must adjacent land uses across the entire watershed be considered? Studies of such scale-dependent relationships between landscape characteristics and water chemistry have yielded mixed results. Johnson et al. (1997) found that total phosphorus in streamwater was better explained by land-use patterns within a 100-m buffer of a stream than by land use or other variables at the extent of the catchment. However, other studies have demonstrated that more distant upland land uses were as important as riparian land uses in larger watersheds (e.g., Omernik et al. 1981), or that whole-watershed predictors performed best (e.g., Nielsen et al. 2012). Responses may also differ between lotic and lentic systems. Gergel et al. (1999) found that landscape characteristics (especially proportion of wetlands) within 50-m of lakes in northern Wisconsin explained significant variability in concentrations of dissolved organic carbon (DOC); in contrast, measurements from the whole watershed always explained more variability for DOC in rivers than did measurements from the nearshore area. Within the Chesapeake Bay watershed, Weller et al. (2011) demonstrated that models that included riparian buffers better explained stream nitrate concentrations than models using only land-cover proportions. Among physiographic regions, the expected reduction in average stream nitrate concentration due to riparian buffers was greatest in the Coastal Plain (50 % of the inputs from cropland) and Piedmont

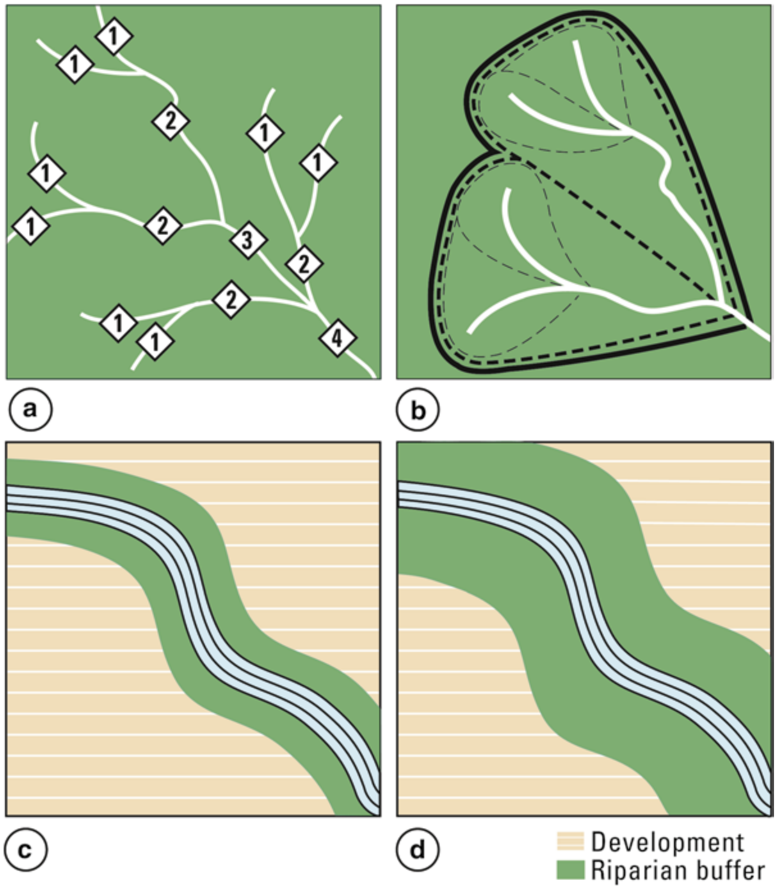


FIGURE 8.13.

Illustration of different spatial extents considered in studies of land–water interactions. (**a**) Hypothetical hierarchical drainage network with subwatersheds; numbers refer to stream order; (**b**) subwatersheds considered separately; (**c**) illustration of fixed-width buffer; and (**d**) larger fixed-width riparian buffer.

(11 %; Weller et al. 2011). In a tropical landscape in Puerto Rico, the spatial scale over which land use and land cover influenced indicators of stream water quality differed across indicators (Uriarte et al. 2011). Turbidity and dissolved oxygen respond to land use and land cover at the watershed scale, in-stream phosphorus concentration and fecal matter content responded at the subwatershed scale, and in-stream nitrogen concentration responded to riparian buffers (Uriarte et al. 2011). The variety of results from studies of watersheds and buffers in different regions underscores the need to better understand the interactions between land and water and the scales over which they are manifest.

The relative importance of spatial configuration (vs. composition) for estimating or managing nutrient loadings to lakes or streams remains unresolved. In general, configuration per se appears to be more important for explaining nutrient loading or concentrations in smaller watersheds than in larger watersheds, where effects of spatial arrangement seem to average out. A study using a grid-based surface-flow simulation model and thousands of simulated watersheds also suggested that the configuration of cover types would be most important in landscapes with intermediate relative abundances of nutrient sources or sinks (Gergel 2005). These simulations suggested an interesting set of hypotheses that relate to percolation thresholds (see Chap. 3) and could be tested empirically (Gergel 2005):

- *In watersheds with <30 % source area*: Increasing fertilizer application rates, increasing heterogeneity, or altering spatial configuration will only slightly alter variability in nutrient loading among different watersheds.
- *In watersheds with >65 % source area*: Spatial location has little impact on nutrient loading; fine-scale heterogeneity in nutrient outputs from source areas markedly affect total loading as the percentage of source area increases.
- *In watersheds with intermediate percentages of source area*: Landscape heterogeneity in sources is expected to influence loading most. Spatial configuration of sources and sinks will matter most, and source output relative to sink uptake will determine the range of source percentages for which this is true.

In sum, land–water interactions are important and complex landscape processes. Components of the landscape surrounding a lake, stream, or river strongly influence water quality. Landscape elements may serve as sources, sinks, or transformers for nutrient, sediment, and pollution loads. Land cover—such as agricultural or urban—is only part of the equation because the actual management practices used on a parcel of land can have very strong effects. Topography also influences the rate of delivery from landscape components to water bodies. When watersheds are steeply sloped and soils are highly erodible, the flux or export of nutrients and sediments to surface waters will increase. In both urban and agricultural landscapes, native vegetation can reduce nonpoint pollution and help maintain satisfactory quality of surface waters.

Mobile Animals and Species Interactions

To understand functional dynamics of entire landscapes, and especially lateral fluxes, interactions between species and ecosystem processes must be considered (Lundberg and Moberg 2003). Grazers can enhance mineral availability by increasing nutrient cycling in patches of their waste (McNaughton et al. 1988) and transport nutrients from one habitat to another (Augustine and Frank 2001; Seagle 2003). Landscape ecology offers a conceptual arena for integrating species and ecosystems that also can help unite the traditionally distinct subdisciplines of population and ecosystem ecology. In an introductory chapter in the book, *Linking Species and Ecosystems* (Jones and Lawton 1995), Grimm (1995) wrote:

> Interactions between population/community and ecosystem ecologists would be facilitated by adopting, *as a starting point*, a spatially based conception of units of study. … Whatever the scale of the investigation, a spatially based perspective places species interactions (the traditional focus of community ecology) into a context in which their effect on ecosystem processes may be assessed. Interactions between patches may be critical to larger-scale processes and include biotic interactions that occur within component subsystems.

Species and ecosystems are inherently linked, but studies in population ecology and ecosystem ecology often ignore this linkage. Landscape studies of lateral nutrient fluxes via animal movement or species interactions provide a clear mandate to bridge this divide.

A considerable body of work has identified animal-mediated movements of materials and nutrients from aquatic to terrestrial communities. Some of these involve large charismatic animals, but aquatic insects can also play important roles. The emergence of midges (Diptera: Chironomidae) and their deposition along the shorelines of Icelandic lakes offer an excellent example of lake-to-land linkages (Gratton et al. 2008). Annual midge input rates were as high as 1200–2500 kg midges ha^{-1} $year^{-1}$. As midges are about 9.2 % total N, the infall of midges was sufficient to fertilize the terrestrial vegetation along some lakes, although this effect declined with distance from the lakeshore. Further, many terrestrial consumers depended on midge-derived trophic pathways (Gratton et al. 2008; Dreyer et al. 2012). In general, insect deposition to terrestrial ecosystems shows a negative exponential decline with distance from shore (Gratton and Vander Zanden 2009), indicating a strong spatial dynamic to this interaction.

Large animals are also important nutrient transfers from water to land. Willson et al. (1998) described an expanded perspective on interactions between fish and wildlife in the Pacific coastal region of North America. Each year, millions of anadromous fish (e.g., salmon, char, and smelt) move from the ocean into numerous freshwater streams to spawn. These fishes provide an important seasonal resource base for a variety of terrestrial predators and scavengers, including bald eagles (*Haliaeetus leucocephalus* and brown and black bears (*Ursus arctos* and *Ursus americanus*, respectively). The anadramous fishes typically die after spawning, and the nutrient subsidies provided by their carcasses to the streams are well recognized. What was surprising, however, was the potential fertilization effects of salmon carcasses on the terrestrial ecosystems (Willson et al. 1998). The predators congregate and feed along the spawning streams in great numbers, then carry salmon, living or dead, onto stream banks and tens of meters into the forests (Fig. 8.14). Marine-derived nutrients, which can be identified by isotopic markers,

Figure 8.14.

Illustration of the movement of nutrients from a stream to fish, bears, and then deposited in the uplands and absorbed into the terrestrial biota.

pass from the bodies of the salmon into the soil and then into the riparian and upland vegetation, with the nutrients probably then moving up the terrestrial food chain. Willson et al. (1998) reported potential additions of P from bear-carried fishes of approximately 6.7 kg/ha, which is similar to the P application rate of commercial fertilizers for evergreens and trees! In southwestern Alaska, bears feeding on salmon increased soil ammonium concentration threefold and nitrous oxide fluxes by 32-fold (Holtgrieve et al. 2009). The consequences of this water-to-land fertilizer effect for terrestrial food webs could have substantial implications for the spatial patterns of ecosystem processes in these forested landscapes. Large mobile consumers can be very important in generating landscape heterogeneity in nutrient cycling.

In terrestrial landscapes, animals that feed in one place but excrete wastes in another location can be important vectors of nutrient transport. The movement of nutrients by large grazers has been recognized for some time, particularly in landscapes such as the Serengeti that harbor large numbers of native ungulates (McNaughton et al. 1988; Seagle and McNaughton 1992). Significant nutrient transfers from croplands to nearby forests by grazers have also been documented (Seagle 2003; Murray et al. 2013). The central-place foraging of birds and bats also results in high concentrations of guano in caves and nesting areas and caves (Stoker 1926; Bird et al. 2007).

Feeding activities of mobile animals can cascade through ecosystems to influence landscape patterns. A set of studies in the boreal forest landscape has demonstrated fascinating links among spatial patterns of plant species distributions and biomass, the foraging dynamics of moose (*Alces alces*), and rates of nutrient cycling (McInnes et al. 1992; Jeffries et al. 1994; Pastor et al. 1997). Studies on Isle Royale, an island located in Lake Superior and well known for long-term studies of moose and wolves, demonstrated how selective foraging by moose on hardwood species allows unbrowsed or lightly browsed conifers to dominate the boreal landscape (McInnes et al. 1992). Moose prefer to browse upon deciduous tree species such as birch (*Betula lutea*) and aspen (*Populus tremuloides*), as well as balsam fir (*Abies balsamea*), rather than on white spruce (*Picea glauca*). In areas of Isle Royale where fences (exclosures) were built to prevent moose from browsing, the deciduous trees have persisted and grown larger. However, outside the exclosures, where moose were allowed to browse, white spruce was the only tree species that could grow above the browsing height of a moose. Moose browsing on balsam fir and the deciduous trees prevented saplings of these preferred forage species from growing into full-sized trees. The browsing of moose also opened up the forest canopy and reduces tree biomass, allowing more light to reach the forest floor and stimulating more production of shrubs and herbaceous species.

Understanding the spatial heterogeneity of ecosystem processes in this boreal landscape requires forging a linkage between the feeding ecology and population dynamics of moose and the function of the ecosystem, all within the context of a landscape. By selectively foraging on specific plant species, moose and other large herbivores influence ecosystem dynamics—changing plant community composition, biomass, production, and nutrient cycling (McInnes et al. 1992). Soils in areas dominated by spruce received less litter, and the nutritional quality of the litter, especially its nitrogen content, declined for the decomposers. This decrease in litter quantity and quality leads to a decline in microbial processes that in turn determine nitrogen availability for the living plants. Conifer litter depresses the availability of soil nitrogen, which limits net primary production in boreal forests.

Moen et al. (1997, 1998) developed a simulation model to predict how alternative moose foraging strategies affect the net annual energy balance and density of moose, and the spatial distribution of browse across the landscape. Simulations were conducted at fine resolution (grid cells of 1 m^2 over an 8-ha landscape), and results have demonstrated how moose “create” their own landscape by their patterns of foraging and the feedbacks of those patterns on vegetation structure and composition. Because moose are highly mobile and can forage all around the landscape, interactions between moose and vegetation create a mosaic of nutrient cycling regimes in these boreal forests resulting in complex spatial and temporal patterns of browsing, conifer density, and soil nitrogen distribution across the landscape (Pastor et al. 1999).

Continued study of this system included a recent decline in the moose population and how that affected browse availability and consumption and soil fertility over an 18-year time frame (De Jager and Pastor 2009). When the moose population declined rapidly, patterns of available and consumed browse became decoupled, in contrast to earlier years. Soil nitrogen availability shifted from repeated to random patterns (De Jager and Pastor 2009).

In sum, species interactions produce strong and persistent patterns of nutrient cycling and accumulation in the landscape. Continued study of spatial interactions of plants and animals is both interesting and necessary if we are to understand ecosystem dynamics at landscape scales.

STATE OF THE SCIENCE: CHALLENGES AND OPPORTUNITIES

Empirical and modeling studies of spatial heterogeneity in ecosystem processes have demonstrated several important points. First, spatial variation in abiotic variables (temperature, precipitation, soils, and topographic position) often produces substantial spatial variation in ecosystem processes. This heterogeneity must be understood because the abiotic template is a powerful driver and constraint of ecosystem dynamics. Second, abiotic factors vary over multiple spatial scales, and ecologists are still striving to determine the scales that are appropriate for developing predictive relationships. Considering these factors hierarchically may enhance our understanding of how they vary. Third, understanding the implications of the dynamic landscape mosaic for ecosystem processes remains a frontier in ecosystem and landscape ecology.

Many empirical studies have taken a comparative approach using integrative measurements, such as nutrient concentrations in aquatic ecosystems, as indicators of how spatial heterogeneity influences the end result of lateral fluxes (Strayer et al. 2003b). Most of these studies focus on nutrients, such as nitrogen or phosphorus, related to surface water quality. Variation in topography, the amount of impervious surfaces (e.g., pavement), and the extent of agricultural and urban land uses have all been related to the concentration or loading of nutrients in waters. However, the particular aspects of spatial heterogeneity that are significant or the spatial scales over which that influence is most important have varied among studies (Gergel et al. 2002). The lack of consistency among the comparative studies may arise, in part, from the need to measure multiple variables changing in space and time and from our limited understanding about how materials actually flow laterally across heterogeneous landscapes.

Additional challenges remain. Scaling microbially regulated processes to entire landscapes remains especially difficult (e.g., Smithwick 2006). Understanding feedbacks from changing vegetation to water, carbon, nitrogen, and phosphorus cycles is an important research need in landscape and global ecology (Wassen et al. 2013). In similar vein, understanding interactions among different vectors remains limited; in semiarid African savannas, nitrogen and phosphorus delivery to riparian zones and the subsequent fate of those nutrients is affected not only by seasonality, hillslope hydrology, but also by fire, flooding, herbivory, and physical disturbance by animals (e.g., wallows; Jacobs et al. 2007). Understanding spatial interactions among interacting drivers and ecosystem elements remains limited.

A landscape perspective continues to offer the opportunity to better link populations and ecosystem processes and services (Lundberg and Moberg 2003); organisms exist in heterogeneous space and they use, transform, and transport matter and energy. Augustine and Frank (2001) demonstrated such an effect by grazers redistributing soil N at every spatial scale from individual plants to landscapes. Seagle (2003) hypothesized that the juxtaposition of land uses with different forage nutrient concentrations interacts nonlinearly with deer behavior to effect nutrient transport of sufficient magnitude to alter ecosystem nutrient budgets. Terrestrial predators, herbivores, and piscivores have all been shown to influence spatial patterns of nutrient pools and fluxes. Considering habitat use and movement patterns of species in a spatial context will continue to provide a wealth of opportunities for enhancing the linkage between species and ecosystems and enhance functional understanding of landscape mosaics.

What can be concluded about when space matters for ecosystem function? Strayer et al. (2003a) proposed a useful conceptualization of model complexity relative to inclusion of spatial and temporal heterogeneity. However, a general understanding of lateral fluxes in landscape mosaics has remained elusive, despite promising conceptual frameworks developed for particular systems (e.g., semiarid landscapes; Ludwig et al. 2000). Spatial heterogeneity is expected to be important for ecosystem processes under several conditions (Turner and Chapin 2005). For point processes, spatial heterogeneity must be considered when it is necessary to know the average rate of a process over an area that is spatially heterogeneous. This is of particular importance when there is a nonlinear relationship between the process and a driver that is spatially variable. Although this is largely a sampling issue—knowing how to stratify measurements spatially based on the important driver(s)—it is *not* trivial. Spatial heterogeneity also matters when one wants to understand or predict the spatial pattern of process rates. One may want to identify locations that are qualitatively different in their processing rates from other areas, or use the spatial pattern or spatial scale of variation as a response variable of direct interest. For lateral transfers, spatial pattern (composition and configuration) is a required predictor variable if the occurrence or rate of a lateral transfer responds directly to spatial heterogeneity. That is, the transfer of materials from one location or patch to another location or patch is modified by the spatial structure of the landscape. Spatial heterogeneity also matters if the spatial patterns themselves generate lateral transfers, as when differences in land cover alter local energy and water balances and influence weather. Finally, lateral transfers may produce, amplify, or moderate heterogeneity in patterns, as when the movement of nutrients from one place to another produces different species distributions or process rates.

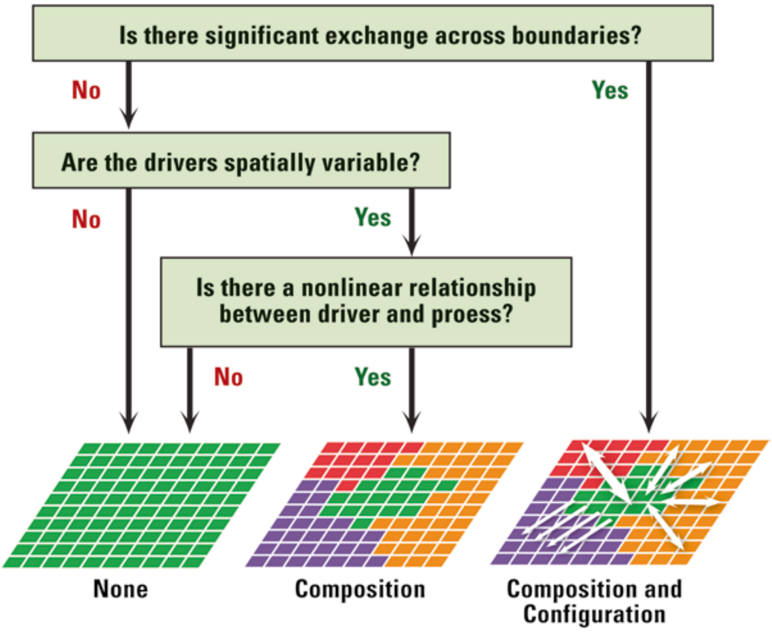


FIGURE 8.15.

Decision tree for deciding whether space should be included in studies of ecosystem function in heterogeneous landscapes that lead to three different general approaches to dealing with spatial heterogeneity: (*left*) assume spatial homogeneity, (*center*) consider composition only using a mosaic approach, which is often multivariate; and (*right*) consider composition, configuration and interacting elements.

ADAPTED FROM TURNER AND CHAPIN (2005) AND LOVETT ET AL. (2005).

A decision tree that emerged from the Cary Conference on ecosystem function in heterogeneous landscapes can provide a useful guideline for ecologists seeking to determine whether a spatially explicit approach is needed for studies of ecosystem dynamics (Fig. 8.15; Lovett et al. 2005). If there are no lateral fluxes, no spatially variable drivers, and no nonlinearities, then perhaps spatial heterogeneity can be safely ignored. If there are nonlinearities, then at a minimum, differences in landscape composition must be considered. And if lateral fluxes are important, both composition and configuration will be required (Fig. 8.15). Much still remains to be learned about ecosystem processes in heterogeneous landscapes. The successful integration of ecosystem ecology with landscape ecology promises a much more complete understanding of how landscapes function than has been developed to date.

SUMMARY

Determining the patterns, causes, and effects of ecosystem function across landscapes is a key topic in ecosystem and landscape ecology because transfers of nutrients and energy among patches are often important for ecosystem sustainability. When landscape ecologists study ecosystem processes, they typically emphasize the causes and consequences of spatial heterogeneity in determining rates of ecosystem processes (e.g., net primary productivity, nitrogen mineralization); the influence of landscape position on ecosystem function; and the horizontal movement of materials (such as water, nutrients, or sediments) across the landscape and how these movements might differ with alternative spatial arrangements of land cover.

The abiotic template is a powerful constraint on ecosystem function, but ecology has lacked a general theory of ecosystem function that is spatially explicit. From a landscape perspective, conceptual frameworks have been proposed that emphasize the importance of boundaries, including their permeability and resistance to flows; subsidies of nutrients and detritus from one habitat to another; extensions of metapopulation and metacommunity concepts to metaecosystems; and distinctions between explaining variation in process rates that are largely vertical fluxes vs. processes that are lateral transfers. In all studies, it is important to be explicit about the ecosystem process as well as the driver or response for which spatial heterogeneity is being considered.

For point processes (i.e., vertical fluxes), much research in landscape ecology has focused on patterns of biomass, net primary production, and carbon, as well as landscape patterns of nutrient biogeochemistry. Strong influences of natural disturbance and land-use/land-cover change on the spatial structure of many nutrient pools and fluxes have been identified. Biotic interactions are also important. Many studies integrate data from a multiple sources and often combine empirical study with modeling. Spatial variability is also observed among the aquatic systems embedded in landscapes, and landscape limnology refers to the spatially explicit study of lakes, streams, and wetlands and the effects of these spatial patterns on ecosystem processes across temporal and spatial scales. Landscape limnology treats the freshwater landscape as embedded in a terrestrial and human mosaic and considers a variety of landscape ecological variables as they apply to freshwater ecosystems: (1) patch characteristics, (2) patch context, (3) patch connectivity and directionality, and (4) spatial scale and hierarchy (Soranno et al. 2010). A landscape perspective also fosters a view of land–water interactions that encompasses sets of lakes, streams, and wetlands occurring together as a connected unit within a landscape.

For lateral fluxes (horizontal transport), research has emphasized aeolian fluxes, such as litter redistribution, land–water interactions, and nutrient transport by mobile animals. Land–water interactions are perhaps the best studied examples of lateral fluxes of nutrients across landscapes because problems associated with eutrophication are so widespread in aquatic ecosystems. Components of the landscape surrounding a lake, stream, or river directly determine water quality and availability—a critical concern as natural landscapes continue to be affected by agricultural and urban development. Elements of the landscape may serve as sources, sinks, or transformers for nutrient, sediment, and pollution loads. A common theme underlying many studies of land–water interactions is the degree to which land uses in the uplands, and the spatial arrangement of these land uses, affect water quality in streams and lakes. Riparian vegetation zones, including wetlands and floodplain forests, are conspicuous elements of many landscapes and important mediators of land–water interactions. The primary emphasis of studies of land–water interactions has been the movement of materials from the terrestrial components of the landscape influences the aquatic components. However, recent studies also have shown that movements of materials and nutrients from the water into terrestrial communities are also significant. These observations provide a strong imperative for ecologists to better understand the reciprocal interactions between land and water and the scales over which they are manifest.

Species and ecosystems are inherently linked, but studies in population ecology and ecosystem ecology often ignore this linkage. Landscape studies of lateral nutrient fluxes as a function of animal movement or species interactions effectively bridge this divide. In terrestrial landscapes, animals that feed in one place but excrete wastes in another location can be important vectors of nutrient transport. Species interactions produce strong and persistent patterns of nutrient cycling and accumulation in the landscape. Continued study of spatial interactions of plants and animals is both interesting and necessary if we are to understand ecosystem dynamics at landscape scales.

Understanding the implications of the dynamic landscape mosaic for ecosystem processes remains a frontier in ecosystem and landscape ecology. We do not have a well-developed theory of ecosystem function that is both spatially explicit and general enough to be widely applicable. However, the library of empirical studies has grown tremendously. New empirical studies are still needed to test hypotheses about nutrient pools, fluxes, and transfers among diverse landscape elements and for upscaling process rates. These challenging issues reinforce the importance of landscape ecology as a conceptual framework for understanding ecosystem function.

DISCUSSION QUESTIONS

1. A daunting challenge in studying spatial variation in ecosystem function and the factors that control the rates of ecosystem processes is balancing data needs (e.g., spatial extent of the study and the ideal number of measurements) with logistical difficulties

and actual cost (e.g., person-hours required for collecting and processing samples and the costs of running laboratory analyses). Consider an extensive landscape of your choice. Develop a field sampling design to describe the spatial variation of an ecosystem attribute or process rate (e.g., NPP, LAI, nitrogen mineralization, denitrification, phosphorus accumulation) of your choice. Then answer the questions below.

(a) *Response variables*. What variables did you decide to measure, and what variables were excluded? How will the choice of variables affect the generality of your results (i.e., application to other landscapes and situations)?

(b) *Sampling design*. Stratified sampling often reduces effort and cost. Did you use stratified sampling in your design? Why or why not? If yes, by what variables did you stratify, and why?

(c) *Spatial autocorrelation*. Many landscape and ecosystem variables are correlated in space and time. Did you consider spatial autocorrelation in your design? How might autocorrelation among variables reduce costs and increase the generality of results?

(d) *Cost*. Estimate the cost of implementing your design in terms of person-hours and laboratory costs (if any). Could costs be reduced by combining remotely sensed data with field measurements? Why or why not?

2. Describe how the processes associated with the release, uptake, and storage of carbon would change in the following scenarios over a period of 100 years (graphical representations may be helpful): (1) a temperate deciduous forest is affected by small-gap disturbances that affect 1 % of the landscape each year and initiate succession within the gaps; (2) a temperate deciduous forest is cleared for agriculture and farmed continuously for 50 years. Farming is then abandoned, and the land undergoes natural succession for the next 50 years; (3) a mature boreal forest landscape experiences wildfire that burns 60 % of the landscape and initiates forest succession. Ten years later, a second fire burns 50 % of the previously burned area and eliminates the newly established trees, resulting in the area of double-burn being dominated by herbaceous vegetation for the next 80 years.

3. Consider an agricultural watershed in which fertilizers are applied to upland crop fields. A management goal for this watershed is to maintain acceptable water quality while producing agricultural products. Under what conditions might a riparian buffer help to maintain water quality? Under what conditions would reduction in the nutrient source (e.g., fertilizers or manure) be needed to maintain water quality?

4. Ecosystem vectors can move materials rapidly and against a gradient. For instance, wind moves dust from Africa to the South of the USA—something that could hardly happen by diffusion alone. Can you develop a set of principles (or “rules of thumb”) to determine for landscape-scale studies of different ecosystem processes when vectors of movement should be considered?

5. Chose an ecosystem function of interest (e.g., carbon loss or accumulation). How do you expect the statistical relationships between a measurement of this ecosystem function and the abiotic variables that control that function to change with spatial scale? Are the changes with scale linear? Why or why not? How does a nonlinear function determine our ability to measure and predict?

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CHAPTER 9

LANDSCAPE DYNAMICS IN A RAPIDLY CHANGING WORLD

Numerous practical applications of landscape ecology can help to define effects of change on ecological systems and prescribe possible solutions. Natural resource managers face many challenges that emerge over entire landscapes. Because these challenges often involve spatial interdependencies among diverse landscape components at multiple scales, comprehensive solutions continue to be pressing needs. Demand for the scientific underpinnings of managing and monitoring landscapes, understanding landscape implications of climate change, considering spatial heterogeneity in land-management decisions, and potentially even designing landscapes to meet ecological and societal goals are widely recognized as essential for conservation and resource management. Consequently, many resource managers are shifting their goals from specific resources such as fish, wildlife, and water to the integrity of entire systems. Research related to ecosystem management (Christensen et al. 1996), sustainability science (Kates et al. 2001), and *ecosystem services*—the benefits provided to people by nature—involves landscape ecology. Ecological effects of land and resource management are sensitive to the temporal scales and spatial configuration of the activity (e.g., timber harvesting or land development). Indeed, nearly all land management agencies in the U.S. have recognized that informed resource-management decisions cannot be made exclusively

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at the level of habitat units or local sites. The demand for applications of landscape ecology has increased so much that it often outpaces the basic science.

Applications of landscape ecology require integration of the many facets of the discipline that have been considered in this book. In managing a particular landscape, consideration must be given to the configuration of the landscape mosaic and how it changes with time, the disturbance regime and its likely consequences for patterns and processes, the responses of many different species that operate at a variety of scales, and effects of landscape change on ecosystem function. Many applications of landscape ecology depend on establishing a cause–effect relationship between landscape composition and/or configuration and a response variable of interest. These relationships can then be used to design landscape mosaics to minimize undesirable impacts. Increasingly, attention is also placed on feedbacks between landscape change and other patterns or processes.

Applied resource management questions were instrumental in catalyzing the development of landscape ecology, and they continue to stimulate both basic and applied research in landscape ecology. For example, understanding the effects of landscape pattern on stream and lake ecosystems was driven by the practical problem of how to reduce non-point-source pollution and maintain healthy aquatic ecosystems. Concern over impacts of habitat loss and fragmentation on biodiversity similarly drove many studies of the effects of landscape pattern on populations and communities. Concern about how climate change, altered disturbance regimes, and land-use change will interact and affect landscape structure and function is driving much current landscape ecological research. The distinction between basic and applied research is often arbitrary; applied problems have basic components, and basic questions have relevant applications. In this chapter, we survey several current environmental challenges in which landscape ecology is playing an important role. We begin with landscape indicators, as they are used in many landscape ecology applications, then consider climate change, land-use change, landscape scenarios, ecosystem services, and landscape sustainability.

LANDSCAPE INDICATORS

Indicators are designed to provide clear signals about something of interest and to communicate information about the status of some property and how it varies over time and/or space (National Research Council 2000). It is often impractical or impossible to measure all of the responses or qualities that may be of interest, and indicators serve as proxies that can be measured more readily. Most of us are familiar with indicators in our everyday lives. Body temperature and blood pressure are indicators of wellness, and gross national product and stock market indices are indicators of economic condition. Similarly, *environmental or ecological indicators* capture information about conditions and trends in the environment and are of practical use in environmental monitoring (National Research Council 2000). For example, the widely used Index of Biotic Integrity (IBI; Karr 1981) incorporates species richness, composition, trophic structure, abundance, and fish condition into a summary index related to the state of aquatic ecosystems. Lake water clarity is another easily measured and well-established indicator of lake water quality that has been incorporated into many citizen-science monitoring efforts (Lottig et al. 2014) and mapped using remotely sensed data (e.g., McCullough et al. 2013) to track regional lake status and trends. Many international organizations have also developed indicators to measure different aspects of biodiversity and assess changes and threats (e.g., UNCED 2007). Indicators can be extremely useful for monitoring environmental trends, detecting changes that might require intervention, tracking the effectiveness of management, and conveying information about environmental conditions and trends to a nonscientific audience. An entire academic journal, Ecological Indicators, is even devoted to the development, use, and interpretation of indicators.

Here, we focus on *landscape indicators*, which quantify the amount and arrangement of land cover and the physical structure of vegetation on the land surface (Gergel et al. 2002), and their application for broad-scale monitoring of landscape state and change. Landscape indicators are typically a subset of landscape metrics (see Chap. 4) that correlate well with other ecological properties of interest, such water quality or wildlife habitat. Time-series data of Earth's surface are now widely available, and repeated imagery can be analyzed to establish baseline conditions and track landscape change. Such analyses can help detect environmental problems as they develop and identify places that may benefit from action. Landscape indicators that emphasize the amount of human-dominated versus natural land covers (Jones et al. 1997) or "distance to nature" (Rüdisser et al. 2012) may be especially useful in tracking landscape status over time.

The U.S. Environmental Protection Agency was an early developer of landscape indicators as part of a national Environmental Monitoring and Assessment Program (O'Neill et al. 1994; National Research Council 2000). The program combined available data sets, such as land cover, major roads, topography, and population density, to quantify landscape changes through time. These changes were then related to ecological variables to determine the potential impact or risk of landscape change. A prototype was developed initially for watersheds in the Chesapeake Bay region (Riitters and Wickham 1995) then expanded to the entire United States. Some analyses emphasized variation from place to place, such as the variation across the continental U.S. in forest fragmentation (Riitters et al. 2002). Kurt Riitters and collaborators calculated the amount of forest along with the amount of "interior" forest in 56-km^2 cells that covered the conterminous U.S., using area of interior forest as a useful indicator of suitable habitat for many area-sensitive species. They identified locations with relatively intact interior forest, but found that most forests had at least moderate levels of fragmentation (Fig. 9.1; Riitters

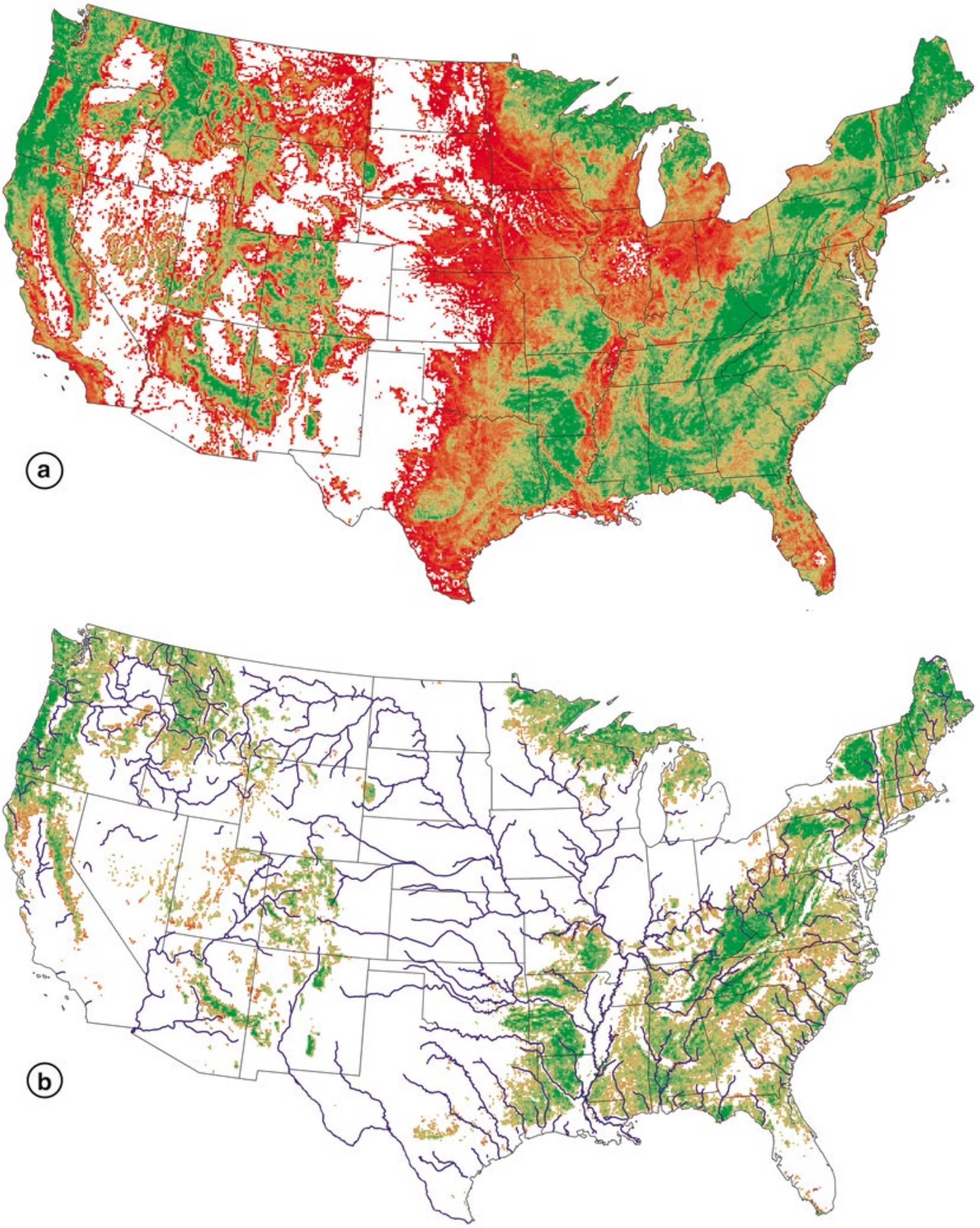


Figure 9.1.

Spatial distribution of (**a**) forest and (**b**) interior forest in the United States. *Shading* represents the relative amount of forest area in 56.25-km^2 grid cells with low forest abundance in red and higher forest abundance in *green*.

From Riitters et al. (2002).

et al. 2002). Interior forest was concentrated mostly on publicly owned lands and on lands not well suited for agriculture or urban development. Broad-scale forest patterns have been the subject of many other landscape studies (e.g., Riitters et al. 2000; Heilman et al. 2002; Theobald et al. 2011). A global analysis indicated that over 50 % of the temperate broadleaf and mixed forest biomes and nearly 25 % of the tropical rainforest biomes have been fragmented by human activities, compared to only 4 % of the boreal forest (Wade et al. 2003); forests of Europe were most fragmented, and forests of South America were least fragmented. Research in forests of northeastern Australia highlighted the need to align the scales at which fragmentation is managed with those at which it is measured (Cattarino et al. 2014).

As data availability and analysis capacity continued to increase, other groups began to advocate for using landscape indicators to monitor regional change. For example, as part of its 2008 report on the STATE OF THE NATION'S ECOSYSTEMS, the H. John Heinz III Center for Science, Economics and the Environment (a non-profit organization that operated from 1995 to 2013) convened a task force chaired by Norm Christensen to develop a suite of indicators for describing broad-scale landscape patterns across the U.S. (Heinz Center 2008). The task force evaluated many potential indicators of landscape pattern and ultimately recommended a set of indicators that quantify landscape composition and configuration and relate closely to known drivers of pattern (i.e., they are sensitive to human development) and expected ecological consequences. The European Biodiversity Observation Network (EBONE; http://www.wageningenur.nl/en/Expertise-Services/Research-Institutes/alterra/Projects/EBONE-2.htm) has also focused on terrestrial monitoring and tracks change in land cover and land-use intensity to relate landscape changes to biodiversity. Securing funding for regular monitoring and reporting of landscape indicators over the long term remains problematic.

A reasonable array of promising landscape indicators has been proposed and demonstrated. To assess effects of agricultural policies on biodiversity in the Austrian landscape, Rüdisser et al. (2012) developed a "simple but smart" set of three indicators: degree of naturalness (N_d), distance to natural habitat (D_n), and its combination in the index, distance to nature (D_2N). The set was designed to measure and describe anthropogenic influences related to land use on ecosystems and habitats and was applied at 25-m spatial resolution across Austria, resulting in a map of naturalness for the country for one point in time (Rüdisser et al. 2012). To assess effects of urbanization in a rural landscape surrounding Columbus, Georgia (USA), Styers et al. (2010) applied a set of landscape indicators expected to relate to ecological condition of soils, streams, riparian zones, and forests. Results were used to rank regional areas based on their overall degree of cumulative environmental impact (Styers et al. 2010). To assess consequences of changing land use and land cover on forests and watersheds in the highlands of New York and New Jersey, USA, Lathrop et al. (2007) used four landscape indicators, each based on landscape composition: percent of altered and unaltered land cover, percent impervious surface cover; percent of riparian zones in altered land covers, and percent interior forest. These were purposefully simple to calculate and easy to communicate. The analyses detected increased impervious surface cover between 1984 and 2000, with the potential for degrading water quality in watersheds that include major reservoirs for drinking water, along with a decline in total and interior forest cover (Lathrop et al. 2007). Notably, this study offered science-based information that actually contributed to passage of legislation aimed at protecting water resources within the region.

Strong relationships between landscape pattern and freshwater quality, along with government directives for sustaining water quality, led to a set of landscape indicators that could assess human impacts on aquatic ecosystems. After reviewing traditional ecological indicators of riverine systems, Gergel et al. (2002) suggested a complementary suite of landscape indicators that related to different aspects of riverine condition, including nutrient concentrations, biotic diversity, channel widening, and woody habitat (Table 9.1). The early work by the US EPA also included indicators related to water quality (Jones et al. 2007). Given the importance of sustaining freshwater resources, and the tight coupling of lakes and streams with their surrounding watershed, metrics that are correlated with water quality and are easy to track over time should be an important component of landscape monitoring.

Terrestrial landscape patterns also can influence coastal ecosystems, and an index of landscape development intensity (LDI; Brown and Vivas 2005) was applied by Oliver et al. (2011) to relate land use/land cover patterns to coral reef condition on St. Croix, US Virgin Islands. Coral reefs are productive, diverse ecosystems that are being degraded in many locations worldwide. Land-use change in coastal landscapes can contribute to this degradation through a variety of mechanisms. Oliver et al. (2011) related the condition of stony corals to LDI values mapped for by watershed and evaluated the strength of the LDI indicator relative to other indicators of human activity. They found the LDI values to be an effective index of human land-use intensity that was significantly correlated with many coral response variables (Fig. 9.2).

The usefulness of any landscape indicator depends on the strength of relationship between the indicator and response or quality of interest; the indicator must be clearly linked to an underlying ecological process. All of the issues of data quality, scale effects, and classification scheme that affect calculation of landscape metrics (see Chap. 4) also come into play for landscape indicators; the analyst or user must be aware of how these sensitivities influence the ability of the indicator to detect real trends over time or differences across space. To guide this process, Rüdisser et al. (2012) suggested several criteria for landscape indicators to be useful in development of sustainable land-use policies:

(A) The indicator set should be a surrogate for anthropogenic impact on biodiversity and not a measure for species richness or biodiversity itself.

Table 9.1.
Comparison of different general types of ecological indicators used to quantify human impacts on rivers.

Indicator	Advantages	Disadvantages
Chemical indicators	Direct measure of in-stream attribute	Can be difficult to collect, store, and analyze
	May be variable among seasons	Citizen-based monitoring may be prone to error
	Citizen monitoring may be economical	Event-based delivery may be missed by routine sampling
Biotic indicators	Biotic indicators may be able to integrate across a variety of taxa and changes in watershed condition	Sampling for invertebrate indicators can be difficult, labor intensive, and samples challenging to process
		Provides qualitative or relative measure
	Indicators based on fish are relatively easy to use in the field	May not provide any indication of why stream is degraded
		Identification of reference sites can be difficult
Hydrological/hydraulic indicators	Long-term flow data are often readily available	Index of Hydrologic Alteration has not been tested in a variety of ecoregional settings
	Indicators can relate physical flows to fish, invertebrate habitat	Wetted perimeter has no explicit representation of habitat
	Have been expanded to include variables beyond fish habitat	Considerable field/analytic work needed for hydraulic measures
Physical habitat	Can provide long-term assessment of geomorphic changes	Labor intensive
	Can be assessed at multiple scales	Measures may not be biologically relevant
Landscape indicators	Can be linked to other types of indicator	Requires some training in the use of GIS and spatial data sources, analyses
	Provide direct measures of human uses in a watershed	Limited to finest resolution of the data
	Can assess very large areas	The most informative spatial extent of indicators still needs to be established
	Data widely available for many areas	
	Data can be stored indefinitely	

Adapted from Gergel et al. (2002).

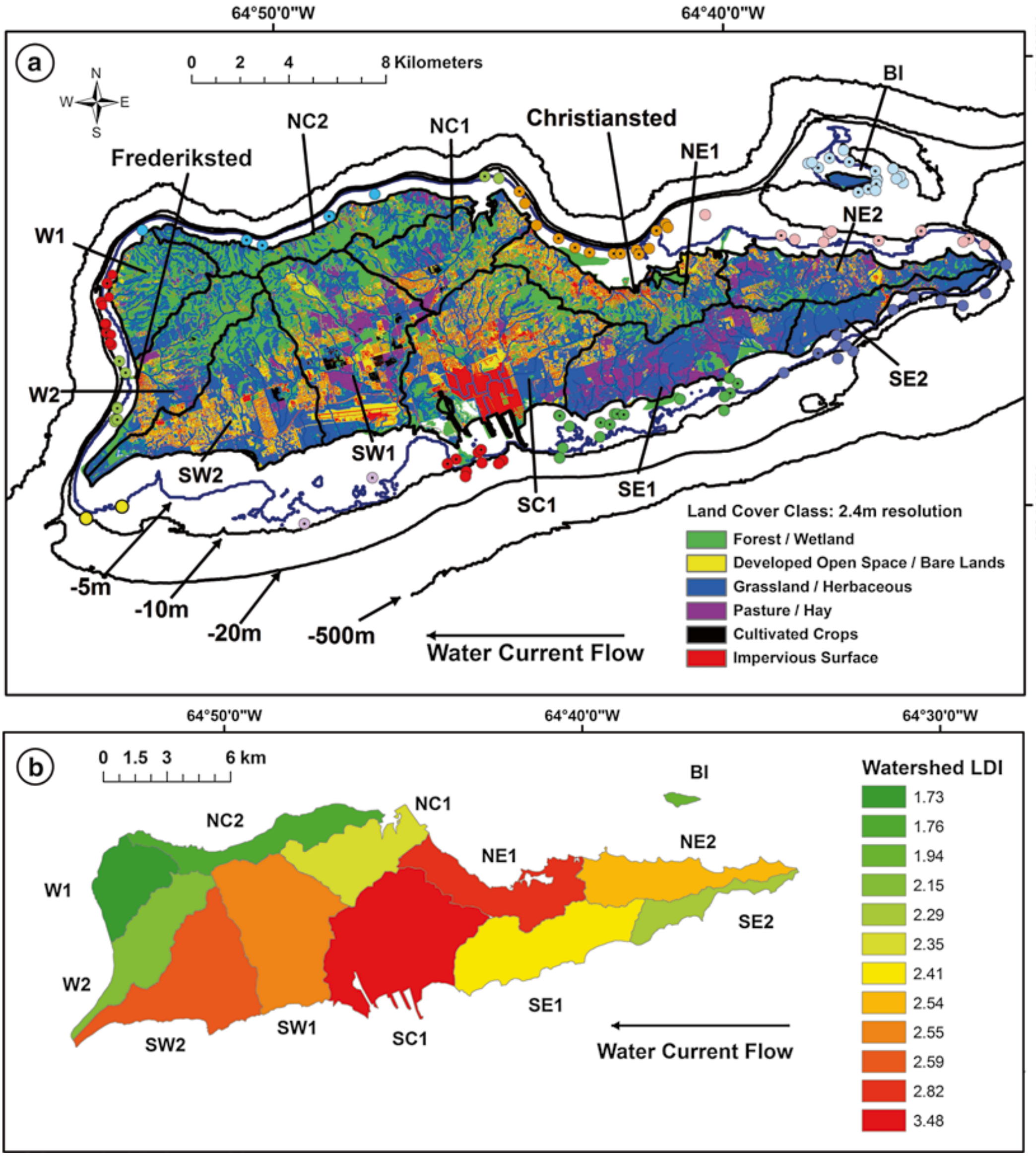


Figure 9.2.

Landscape patterns on St. Croix, US Virgin Islands, were related to status of coral reefs. Pattern of (**a**) land use/land cover on St. Croix and (**b**) watershed landscape development intensity (LCI) values with *green* indicate lowest human disturbance and *red* the highest. Relationship of LDI and (**c**) coral colony density, (**d**) taxa richness, (**e**) average colony surface area, and (**f**) three-dimensional cover (3DTC). Pearson correlation coefficients are indicated with accompanying *p* values, and bold coefficient is the result if the outlier is removed. Maps and data reprinted with permission from Oliver et al. (2011). Photo from US National Oceanic and Atmospheric Administration, licensed through Creative Commons.

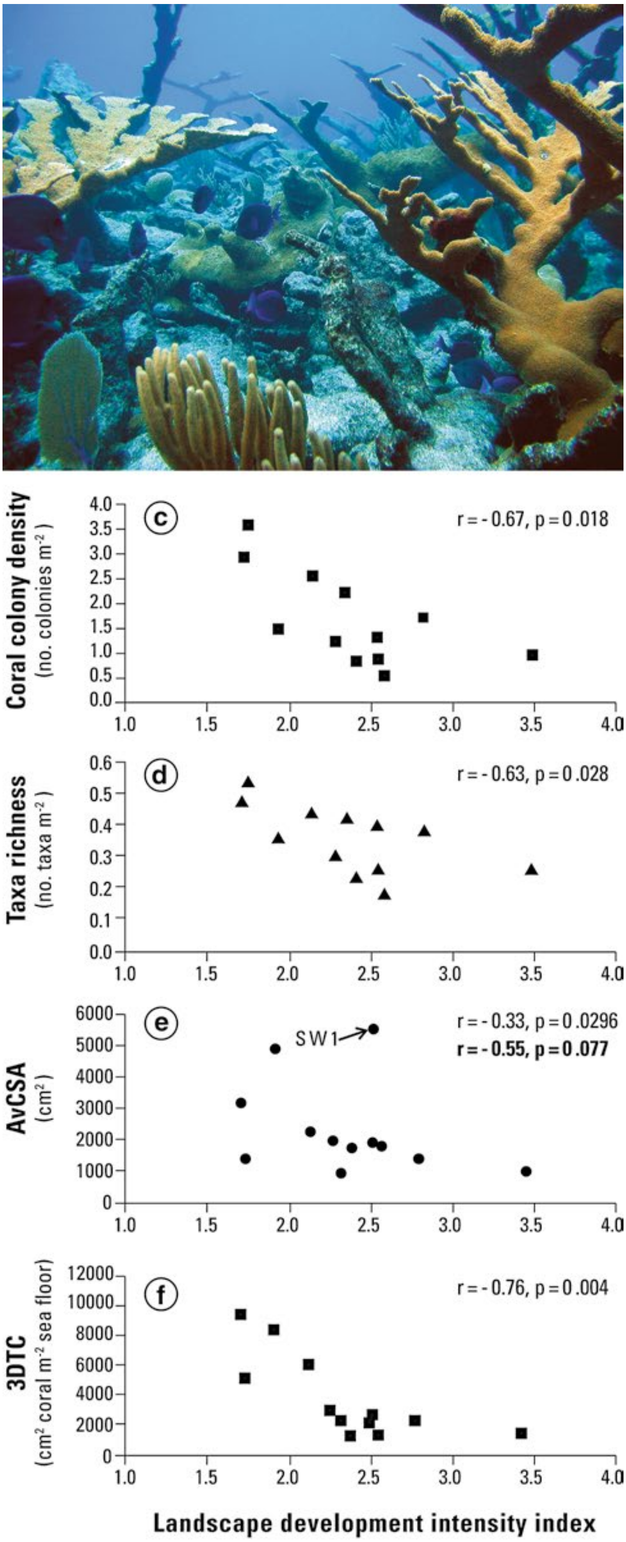


FIGURE 9.2.

(continued)

(B) The indicator set should serve to evaluate and compare biodiversity relevant land-use characteristics at a small-scaled spatial resolution while covering an extensive area.
(C) Indicator estimation should be spatially comprehensive, independent from reporting units and based on already existing data ensuring comparability at different spatial scales (regional to international).
(D) To ensure international comparability, indicator estimation based on land-use data with different thematic and spatial resolution should be proportional, even though less detailed.
(E) The design should be comprehensible, facilitating interpretation and communication of indicator results.

As we've seen throughout this book, landscape pattern affects many ecological attributes and human values, and rapid changes are expected in the twenty-first century as climate warms, population grows, and resource consumption patterns change. As part of the toolkit of applied landscape ecology, landscape indicators should remain a part of any monitoring program to detect and quantify regional ecological change.

CLIMATE CHANGE

The *climate* of a region is measured as the long-term average of the suite of meteorological variables used to describe weather—measurements of temperature, humidity, precipitation, wind, and atmospheric pressure. *Weather* variables, in turn, are short-term measures of the energy and water availability within a given region. When climate variables are combined with a description of regional landforms it is possible to predict the potential ecosystem types one may expect to find within that region (Bailey 2009). Consequently, changes in climate and/or landscape structure are expected to change the type, distribution, and structure of ecosystems around the globe (Blois et al. 2013; Moritz and Agudo 2013).

Climate may change slowly with periodic shifts in solar radiation and geophysical forces that alter the physical properties of a landscape (e.g., soil development and erosion, river formation, volcanos and tectonic events, etc.). More rapid changes in climate are now being produced by a variety of human activities (Diffenbaugh and Field 2013; Melillo et al. 2014) with the primary drivers being the release of greenhouse gases (Allen et al. 2010) and land-use change (Feddema et al. 2005; Pielke 2005). The potential variety and severity of biological effects resulting from climate change include shifts in species distributions and changes in ecosystem processes and services. Although the agents of accelerated climate change are generally understood, the rates of change and severity of impacts remain uncertain (Heal and Kriström 2002; IPCC 2013; Knutti and Sedláček 2013) making this subject area both important and controversial. We limit our discussion here to a few examples that are highly relevant to landscapes ecology.

The two principle anthropogenic agents of change—increased levels of solids and greenhouse gases in the atmosphere (Molina et al. 2014) and rapid changes in land use and cover (Pielke 2005)—have together increased the heat-absorbing capacity of the atmosphere, altered hydrologic cycles (Pyke 2004), and shifted the landscape's albedo, i.e., the reflectivity of the earth's surface (Feddema et al. 2005). Records show that changes in temperature and shifts in water availability have already caused detectable shifts in species distributions (Crimmins et al. 2011), threatened agricultural production (Fedoroff et al. 2010; Wheeler and von Braun 2013), and raised concerns for the sustainability of water supplies for human consumption (Vorosmarty et al. 2000). Near-term projections of climate shifts are expected to affect the location and extent of critical habitat areas, such as wetlands in the Northern Prairie, which are expected to decline in size and may locally disappear (Johnson et al. 2005). Species residing at higher elevations are at risk due to warming, with a ~60 % loss of endemic birds expected in mountain areas of Indonesia (Harris et al. 2014). Protected areas may be drastically altered by climate change, requiring changes in conservation strategies to protect migrating birds (Bellisario et al. 2014). Because forests cover ~30 % of land surfaces and store ~45 % of terrestrial carbon (Bonan 2008), and are a significant source of fuel and fiber, changes to forested ecosystems due to climate change have long been of concern (e.g., Solomon 1986; Pastor and Post 1988). The direct effect of increased temperatures and atmospheric CO_2 may enhance productivity in some areas while altering species compositions and causing a northward shift of temperate and boreal forest zones (Kirilenko and Sedjo 2007; Boyd et al. 2013). Indirect effects on forests are more difficult to anticipate, but changes in water availability and increases in disturbances, especially fire and insect pests (Boyd et al. 2013; Diffenbaugh and Field 2013), have already affected many forested areas (Littell et al. 2010). Paradoxically, reduced levels of outbreaks of the spruce bud worm may occur in eastern Canada if climate change causes minimum temperatures to increase with time (Zhang et al. 2014).

Potential impacts of climate change on agricultural production are of serious concern, especially for regions of the globe where food shortages currently exist (Wheeler and von Braun 2013). Projections from climate models show that crop yields are likely to be negatively affected in tropical areas where relatively small increases in temperature may exceed tolerance limits for photosynthesis (Wheeler and von Braun 2013). Temperate zones that experience significant levels of warming are expected to have equally dire effects. We know that warmer temperatures in Europe in the summer of 2003, when average temperatures were ~3.5 °C higher than normal, resulted in crop yield reductions of 20–30 % (Fedoroff et al. 2010). However, the nature and severity of effects of climate change are crop dependent, with some crops in some regions benefiting from increased levels of atmospheric CO_2 (e.g., barley in East Africa and sugarcane in Central America, Lobell et al. 2008) while crops grown in drought-prone regions may be negatively affected by increasing limits of available water (Field et al. 2007). These positive and negative effects are expected to cause significant shifts in agricultural practices and geographical locations where specific crops may be grown, threatening food security for millions of people (Lobell et al. 2008). The continued loss of productive lands to urbanization will, however, make the geographical relocation of agricultural areas problematic (Fedoroff et al. 2010).

Crops grown in regions currently near climatic thresholds are most likely to suffer from climate change. Winegrapes in California are a particularly good example of crop-dependent vulnerabilities (Hayhoe et al. 2004): the values of wine production in California exceed $23 billion per year (Wine Institute, www.wineinstitute.org) creating an industry-wide interest in the economics of climate change with detailed weather records providing insights into potential climate change effects on winegrape production. Wine production is also of broad interest because high-valued wines are produced in the Mediterranean climate region that is a global biodiversity hotspot (Hannah et al. 2013) making climate-induced changes in viticulture an economic indicator of associated risks for many other species and crops (Hannah et al. 2013).

Assessments of future climate trends indicate a projected 25 % decrease in area for winegrape production in Chile and as much as 73 % decrease in Australia (Hannah et al. 2013). However, detailed weather and wine production records over the period 1951–1997 in California's Napa and Sonoma Valley (NSV), where premium wines are grown, have shown counterintuitive effects. There has been a 1.13 °C increase in average temperatures in NSV with a significant reduction in frost frequency associated with a 2.06 °C increase in spring temperatures (Nemani et al. 2001). These small changes have had an impact on plant phenology with more successful flowering, earlier harvests, and larger crops. In addition, measures of wine quality at harvest improved significantly over the period 1963–1996 (Nemani et al. 2001).

This "good news" is tempered by climate projections for the next 50 years, which show dramatic changes in suitable winegrape areas throughout California (Diffenbaugh et al. 2011). Moving vineyards to new places in the landscape as climate conditions continue to change is likely because demand for wine is expected to continue growing, in part due to increasing wine exports to China (Anderson and Wittwer 2013). In California, vineyards would likely shift to more moderate climates at higher elevations and/or along the Pacific coast (Diffenbaugh et al. 2011). However, moving vineyards is economically and ecologically expensive due to habitat loss and increased water demands required to establish new vineyards (Hannah et al. 2013).

Migration in Response to Climate Change

The evolution of physiological traits that has occurred over 1000s of years determines the ecological conditions where plants and animals may flourish. When changing climate modifies local environmental conditions (e.g., light, temperature, moisture, etc.), a species must either relocate to remain within its optimal environment or adapt to altered environmental conditions to avoid local extirpation (Pitelka et al. 1997). Knowledge of these processes has allowed us to explain current patterns of the distribution of the earth's biota (Richardson and Bond 1991; Pitelka et al. 1997). The accelerating rate of climate change makes the possibility of species adaptation or movement uncertain (Davis and Shaw 2001; Corlett and Westcott 2013; Renton et al. 2013).

Paleoecological records clearly show that some species may move quickly over long distances (Clark et al. 1998). However, extensive habitat fragmentation makes the probability of successful migration difficult to estimate (Travis 2003). A variety of theoretical methods—including percolation theory (Chap. 3) and network theory (Urban and Keitt 2001; Baranyi et al. 2011)—show that thresholds exist where small changes in landscape pattern can have disproportionate effects on dispersal success (Fig. 9.3). Although these studies are based on theoretical principles, simulation studies with empirically derived, species-specific parameters have

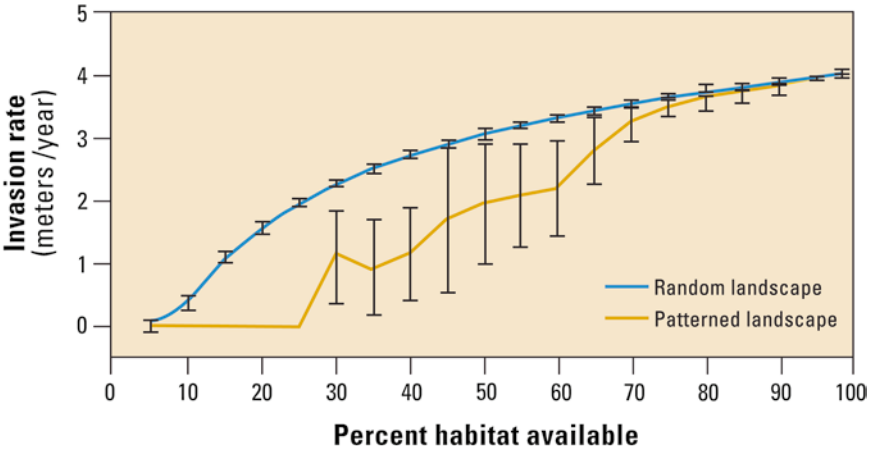


FIGURE 9.3.

Habitat alteration can constrain the movement of plants through a landscape dependent on the pattern of suitable sites that may support plant growth. This neutral model example (Chap. 3) contrasts movement of an annual plant species whose propagules are spread according to an exponential distribution (mean distance of 1 m and a maximum range of 6 m) through a random (*blue line*) and patterned landscape (*yellow line*). A fractal algorithm was used to generate the patterned map. The rate of invasion (with bars representing 95 % confidence intervals from ten iterations) slows more rapidly in patterned maps because connectance between habitat patches is easily disrupted.

ADAPTED FROM PITELKA ET AL. (1997).

verified the existence of these thresholds (e.g., Bunn et al. 2000; Lookingbill et al. 2010). The good news is that simulation methods have also demonstrated specific pathways that may allow species movement through disrupted landscapes. The maintenance and/or restoration of these pathways can be shown to maintain viable populations via dispersal and establishment processes as the climate alters the locations of suitable habitat (Renton et al. 2012).

Migratory species in general, and birds in particular, already require a network of suitable habitats for feeding and nesting. Effects of climate change that alter any of these widely distributed resources threaten even these organisms that are capable of dispersing quickly over large distances (Bellisario et al. 2014). A recent review and synthesis of climate effects indicates that the majority of North American bird species (314 of 588 species) will be forced to find new places to live, feed, and breed over the next 65 years (Nijhuis 2014). Indirect effects through climate-induced changes to food webs may be a critical factor for many species (Wolf et al. 2010). For instance, puffins successfully reintroduced off the Maine coast now show declining numbers perhaps due to changes in the ocean food web (http://blog.nwf.org/2013/06/climate-change-spells-peril-for-puffins/). The threats of increased extinctions are real, although the rate and degree of change remains uncertain.

Empirical verification of changing climate effects on species' distributions is difficult to obtain when landscapes change in response to multiple drivers. However, empirical information generally does support the results obtained by simulation methods. For example, records for 30 years of rapid climate warming in the UK and distributions for a variety of animal species (Fig. 9.4) showed that most species'

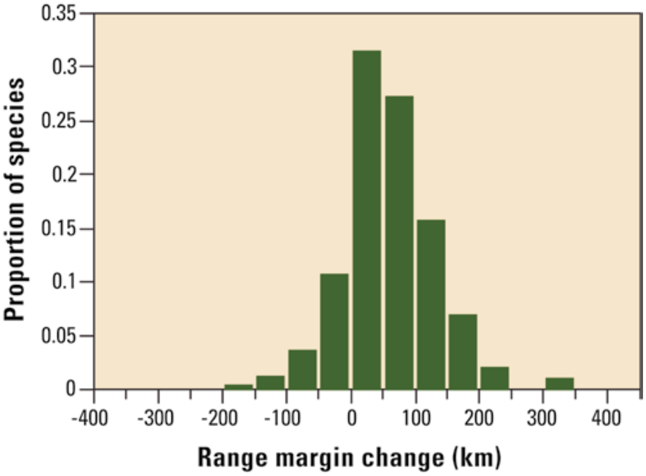


FIGURE 9.4.

Shifts at the northern range boundaries of southerly distributed animal species in Britain. Northwards shifts are positive values, and southwards shifts are negative, with distances moved over approximately 25 years.

ADAPTED FROM THOMAS (2010).

boundaries have shifted northward as climate warmed (Thomas 2010). These observed shifts were attributed to both the direct effects of climate change and indirect effects associated with species interactions (Thomas 2010).

Climate Effects on Disturbances

The frequency, severity, and extent of disturbances are likely to be altered dramatically by climate change (Littell et al. 2010; Turner 2010; Iverson et al. 2011). Climate-induced changes in disturbance regimes will in turn produce immediate and long-lasting shifts in ecosystems with associated changes in ecosystem services (Bonan 2008; Turner 2010). The interaction of different disturbance types, such as drought and insect disturbances, is already affecting large areas of mountain forests in the western United States making disturbed forests a short-term net carbon source (Kurz et al. 2009), although regional carbon balance must be considered over an entire disturbance cycle. Consequently, understanding future disturbance regimes will be increasingly critical for managing and adapting to the effects of climate change (Turner 2010). This important topic has been more fully discussed in Chap. 6, and we touch on it later in this chapter with regard to interacting drivers.

LAND-USE CHANGE AND LANDSCAPE SCENARIOS

Throughout the world, land cover today is being directly altered by human activities, including agriculture, raising of livestock, forest harvesting, settlement, construction, mining, and energy production (Dale et al. 2000). As human populations and their demands for resources increase, natural ecosystems are sequentially transformed to meet increasing societal demands that follow a predictable sequence called the *land-use transition* (Foley et al. 2005). At the outset, frontier clearings perforate natural ecosystems, and then urban areas and intensive agriculture gradually increase as populations grow and resource demands increase (Fig. 9.5; Foley et al. 2005). The extent of unmodified ecosystems declines as the landscape becomes dominated by human uses, although some areas may be set aside for conservation or recreation. This sequence has been observed worldwide, although timing, location, and rates of transition differ. Over the past two centuries, the total land area dedicated to human uses has grown dramatically, and increasing production of goods and services has intensified both use and control of the land (Richards 1990).

Land-use activities change landscape structure by altering the relative abundances of natural habitats and introducing new land-cover types. Introduction of new cover types can increase biodiversity by providing unique habitats, but the amount and connectivity of natural habitats are often reduced, leaving less area

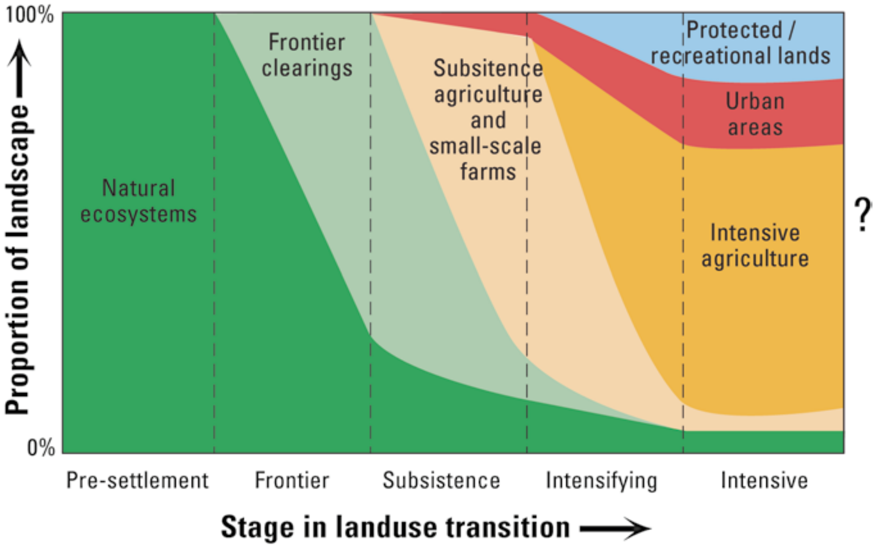


FIGURE 9.5.
Stages in the land-use transition are observed in a given region over time. Land-use regimes vary from presettlement natural vegetation, to frontier clearing, subsistence agriculture, and then more intensive agriculture, urban lands, and protected areas.

ADAPTED FROM FOLEY ET AL. (2005).

available for native species. For example, land-use change has reduced forest connectivity in the western US, where only about one-fourth of forested lands remain in core patches (Theobald et al. 2011). Loss and fragmentation of once-continuous habitat often results in reduced diversity of native species. Understanding land-use changes and their ecological implications presents a fundamental challenge to ecologists and one in which landscape ecology clearly must play a role.

The rate of land-cover change has accelerated worldwide, particularly in regions with rapid population growth. Forests and grasslands have undergone especially large alterations (Houghton 1995). For example, between 1700 and 1980, the area of forests and woodlands decreased globally by 19 %, and grasslands and pastures diminished by 8 % while world croplands increased by 466 % (Richards 1990). The pace of change continues to accelerate, with greater loss of forests and grasslands during the 30 years from 1950 to 1980 than in the 150 years between 1700 and 1850. Croplands and pastures now occupy roughly 40 % of the land surface (Foley et al. 2005), and the terrestrial biosphere is now mostly anthropogenic (Ellis et al. 2010b).

Because land-use activities have transformed such a large proportion of the land surface on Earth, the global consequences of changing patterns of land use and land cover (LULC) are profound (DeFries et al. 2004; Foley et al. 2005). Accordingly, the Ecological Society of America, as part of the Sustainable Biosphere Initiative, sponsored an in-depth discussion of principles and guidelines for land use (Dale et al. 2000). Land is transformed intentionally to provide resources for human consumption, but unintended consequences for water, human health, and biodiversity also result—and balancing these demands is not easy. LULC patterns directly affect local areas, but their influence via consequences of landscape context for ecological responses can be very large.

Land use is an outcome of human–environment interactions, and dealing with causes or consequences of land use thus requires treating landscapes as coupled *social–ecological systems* (SES). Land use offers a common ground for integrating natural and social sciences, which often seem to diverge because of their different research tradition. Billie Turner and Paul Robbins (2008) provided a very insightful comparison of land-change science and political ecology, capturing key similarities and differences in natural and social science approaches to landscape change; we highly recommend this paper for interested readers.

Understanding the ecology of urban landscapes is a topic of much current interest, and research on urban ecology has burgeoned in the past decade (Wu 2014). The land area dominated by cities is a small percentage of the global land surface, but more than half of the world's population now lives in urban areas (Wu 2008), and cities account for a very large share of global resource use. Cities are socio-ecological systems that are built by and for humans. Although urban land cover is included in landscape analyses and urban ecology does have a long history, cities were not traditional settings for most ecological research because of the view that cities were "ecologically unnatural" or impaired. This exclusive emphasis on natural systems has changed with increased attention to urban landscapes, and it now seems imperative to study ecological dynamics where people live and work. Much research on urban sustainability focuses on human well-being, but urban ecological studies emphasize biodiversity, ecological processes, and ecosystem services (Wu 2014). Richard Forman, a pioneer and long-time leader in landscape ecology, devoted an entire book to urban ecology (Forman 2014); he includes spatial aspects and presents a very comprehensive look at cities.

A recent assessment of urban areas in the United Kingdom identified a number of explicitly spatial aspects of cities that are important but challenging to manage (Gaston et al. 2013). The type and arrangement of *green space* (which they define as any area of land not covered by impermeable surface, including remnant vegetation, public parks, public and private landscaping, domestic gardens, playing fields, cemeteries, nature reserves) is very important for providing ecosystem services to urban dwellers. However, most urban green spaces are small and heterogeneous because of the many different uses to which these parcels are put and the variety of land ownerships (e.g., public or private; Gaston et al. 2013). Even if seminatural habitats are scant, urban areas can offer some surprising benefits with respect to their role in the landscape. In the conterminous US, human settlements can store as much carbon (23–42 kg C m^{-2} in urban areas, and 7–16 kg C m^{-2} in exurban areas) as tropical forests, which have the highest carbon density of natural ecosystems (Churkina et al. 2010)!

Urbanization may be a homogenizing force, producing ecosystems and landscapes that are more similar to each other than to the natural ecosystems that they have replaced. In a comparative study of six urban areas, Groffman et al. (2014) hypothesized that similarity in people's decision-making processes would promote convergence and homogenization in urban ecosystem structure and function, even if the biophysical landscape settings were different. In other words, the lawns, yards, and impervious features that are common elements in different cities would be more similar to each other than to the desert, prairie, or forest ecosystems that were replaced by urban development. Indeed, this was the case. Urban areas in Miami, Florida, and Phoenix, Arizona, which are subtropical and desert locations, respectively, were very similar, despite the stark differences in their natural landscapes (Fig. 9.6.) This similarity also suggested the potential for convergence in landscape functions including ecohydrology (Groffman et al. 2014).

Rural landscapes are changing in many parts of the world. Ancient Chinese agricultural village landscapes, which cover about 20 % of China's land area, have been greatly transformed in the past 50 years by social, technological, and ecological changes (Ellis et al. 2009). Between 1945 and 2002, village populations nearly doubled, and per capita housing density declined in China's rural areas. These were accompanied by a 7 % increase in built surface areas, a 9 % increase in cover of closed-canopy trees, and an 11 % decline in annual crops (Ellis et al. 2009). What is particularly interesting is that these changes were driven by fine-scale land-use changes that included tree planting, improved forestry, abandonment of some cropland, and adoption of perennial crops. Analyses based only on coarse-resolution data would miss these important land transformations (Ellis et al. 2009); because they cover such a large area, these local landscape changes can be of global import.

Low-density rural housing development has been the fastest-growing land use in the US since 1950. The conterminous US had about 5 % of land at exurban housing densities in 1950, and exurban areas increased to occupy 25 % of the landscape by 2000 (Brown et al. 2005). By comparison, urban area increased from 1 to 2 % of the land area during the same interval. Most exurbanization occurred outside but near existing metropolitan areas, and this housing growth was often associated with declines in cropland. The ecological implications of increased exurbanization and the associated increase in wildland–urban interface (WUI; Radeloff et al. 2005) have garnered considerable attention, especially evaluation of associated effects on biodiversity.

Landscape ecologists were among the first scientists to recognize the need for more holistic approaches to understand and conserve habitats across the rural-to-urban development gradient (e.g., Miller and Hobbs 2002), and they continue to advance this field (e.g., McDonnell and Hahs 2008). Across taxa, responses to development density are species specific, and species richness for some taxa can be

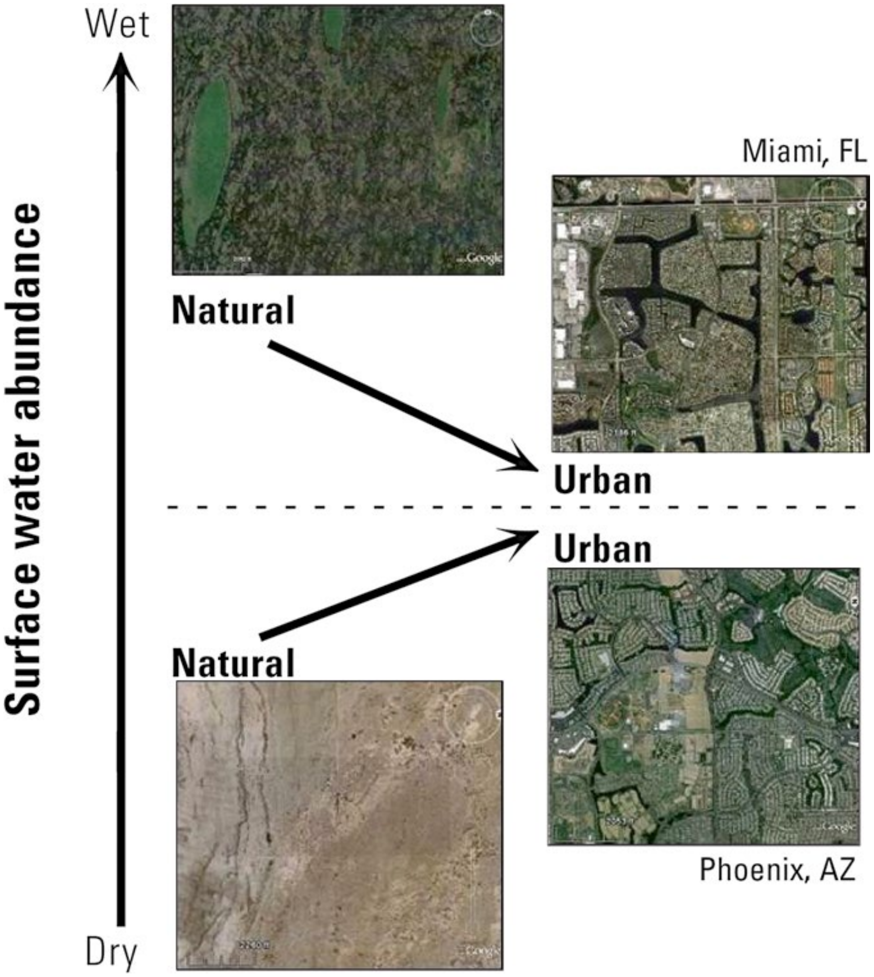


FIGURE 9.6.

In Miami, Florida and Phoenix, Arizona, Urban homogenization makes cities more similar to each other than they are to the native vegetation that is replaced by urbanization. Examples shown for subtropical Miami, FL, and desert Phoenix, AZ.

FROM GROFFMAN ET AL. (2014), REPRINTED WITH PERMISSION.

high at moderate levels of development because of contrasting biodiversity response patterns along the rural-to-urban gradient. Native species may decline as development proceeds, but nonnative species often increase (Hansen et al. 2005); species richness, if considered alone, is unlikely to be the best indicator of how biodiversity is changing.

Hansen et al. (2005) hypothesized that different guilds of organisms would respond to increasing rural residential development in different ways (Fig. 9.7), and a large body of research is helping to guide development in ways that reduce

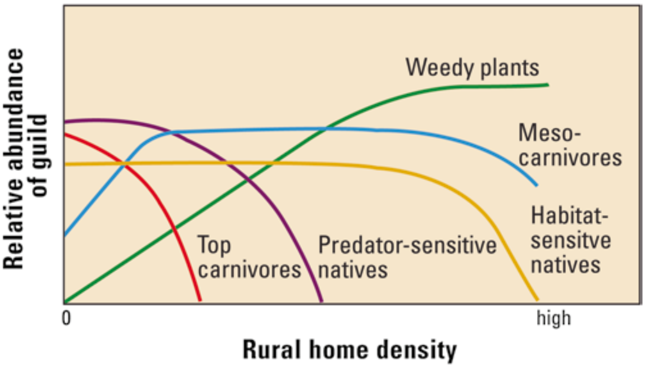


Figure 9.7. Hypothesized responses of different guilds of species to increasing rural home density.

Adapted from Hansen et al. (2005).

negative effects on native species. In Colorado, wildlife cameras were used to assess mammalian habitat use with varying densities and configurations of housing development (Goad et al. 2014). Results were used to inform development planning so that impacts to mammals could be reduced. In the Greater Yellowstone Ecosystem (GYE), low-density residential development creates sink habitats for grizzly bears (*Ursos arctos*; Schwartz et al. 2012), and future expansion of exurban development was projected to impact many wildlife populations. However, spatial policies that clustered development near towns and avoided development in sensitive habitats, such as riparian areas, could mitigate impacts on native wildlife (Gude et al. 2007).

Expansion of development into disturbance-prone landscapes is continuing to increase the conflict between human and natural values. This is especially evident in locations where low-density housing has crept into conifer forests that burn regularly. Although not ecologically catastrophic, infrequent, severe fires can lead to substantial property loss, and fire-fighting efforts to protect developments in fire-prone regions endanger the lives of responders. Future land-use choices must be informed by expectations for how landscapes are likely to change in the future, but increased conflict between land-use patterns and changing disturbance regimes seems likely (Turner 2010).

Land-use changes outside the boundaries of national parks and protected areas may alter biodiversity and ecological processes within such reserves (Hansen and DeFries 2007). In concert with climate change, human activities on surrounding lands often endanger the biodiversity of those protected areas. Protected areas can become "islands" in a "sea" of development, and thus conservation activities cannot ignore the regional landscapes in which those reserves are embedded. The landscapes around most US national parks have experienced substantial changes, including increased housing density, temperatures, and nonnative plant species (Hansen et al. 2014). Some national parks benefit from a buffer zone of additional wildland protection outside their boundaries, but development or extractive resource use go right to the edge of others. Cumming et al. (2014) have recognized this trend by considering protected areas in a social–ecological systems framework, emphasizing the importance of maintaining functional landscapes for long-term sustainability of protected areas and reserves.

Of course, landscapes are not affected by single factors acting individually and independently. Rather, landscapes respond to multiple factors acting across a wide range of scales and which may interact. Effects on landscape structure must be considered when decisions about development locations, densities, and uses of the land are made. However, understanding the relative importance of different drivers and their potential to interact to change our landscapes in surprising ways is scant. In a study that considered both climate and land-use change, Ordonez et al. (2014) assessed the combined speeds of climate and land-use change for the conterminous US from 2001 to 2051. Climate speeds were substantially higher than land-use speeds in most regions, but land-use speed was high in north-central forests and in the Appalachian Mountains. The analysis identified areas that were expected to be most vulnerable to changes in biodiversity and ecosystem function over the 5-year study period in response to these drivers. Further, the study underscored the need for different adaptation programs in different landscapes and clearly showed that considering single drivers will be insufficient for achieving conservation goals (Ordonez et al. 2014). Nassauer and Opdam (2008) raised the importance of *design*—any intentional change of landscape pattern for the purpose of sustainably providing ecosystem services while recognizably meeting societal needs and respecting societal values—to bridge the gap between knowledge and practice in landscape ecology. A key challenge—and opportunity—for landscape ecologists is to elucidate the relative influence of different drivers and the degree to which LULC patterns can be purposefully designed to mitigate environmental problems.

Landscape Scenarios

Determining what patterns of land use will be in the future or should be to optimize oft-competing goals is not easy, and predicting future LULC is fraught with difficulty. As we saw in Chap. 2, the pattern of any given landscape is but one of many possible outcomes (Phillips 2007), and landscape patterns reflect multivariate causation, multiscale drivers, and numerous contingencies. Blithely extrapolating past trends into the future is dangerous because so many unpredictable factors can influence future outcomes. Confounding the issue, known drivers of LULC change often cannot be measured directly, or they may not be measured at scales relevant for predicting emerging patterns. External drivers, for example, include commodity prices, global markets, macroeconomic trends, and social preferences. Events that are inherently unpredictable, such as the onset, magnitude, and timing of recessions; structural changes in job markets; boom-and-bust cycles in housing markets; and even disease outbreaks, may be important drivers determining future landscapes. Many drivers are also not stationary over time (e.g., Wear et al. 1996), thus making it risky to extrapolate past trends into the future, although extrapolation can be useful for exploring the logical consequences of such continued trends. For example, using only a single 5-year window of time for estimating rates of change, Radeloff et al. (2012) found that 36 % of the US land area would change by 2051 if these rates were linearly extrapolated. These extrapolations can be useful, but rates rarely remain constant over time and, therefore, such extrapolations should never be regarded as functional predictions of the future state of a landscape.

In response to the need to anticipate future conditions in the face of tremendous uncertainty, *scenarios* have proven very useful for exploring implications of changes in land use and other drivers of landscape pattern. Scenarios are plausible accounts of possible futures (Peterson et al. 2003; Polasky et al. 2011), and their aim is not to predict what will happen in the future. Rather, the role of scenarios is to define important cause–effect variables, to explore their uncertainties, and to shed light on the possible consequences of decisions and consider trajectories that encompass both desirable and undesirable outcomes. Alcamo et al. (2005) called scenarios descriptions of how the future may unfold based on alternative if–then propositions. *Quantitative landscape scenarios* are common tools in landscape ecology studies. They are usually spatially explicit representations of future or alternative LULC patterns that allow landscape structure to be quantified and potential ecological consequences assessed. Quantitative landscape scenarios compare the composition, configuration, and location of different LULC classes among scenarios at a specified time or endpoint (e.g., 50 years into the future), or they may compare actual trajectories of change (i.e., the time series).

Different types of quantitative landscape scenario serve different purposes; readers might consult Nassauer and Corry (2004) and Houet et al. (2010) for more detail. Briefly, *projective scenarios* describe what the future is likely to be, with a confidence interval of uncertainty. If current trends continue, what will the landscape look like in the future? In essence, projective scenarios extend the past into the future and are useful for demonstrating longer-term consequences of recent or current decisions (Table 9.2). In contrast, *prospective scenarios* describe how the future could be, and what might be a reachable future. Prospective scenarios may be forecasts that use quantitative, dynamic models to project future outcomes of alternative policies or rules, and *explorative scenarios* evaluate the consequences of different decisions. Prospective scenarios may also be *normative*, in that they evaluate alternative solutions to suggest what should be done to reach a desirable goal. The purpose of normative scenarios is to inspire policy, to suggest pathways to reach desired outcomes (Nassauer and Corry 2004; Houet et al. 2010).

In the remainder of this section, we present examples that integrate landscape ecology with future scenarios that include LULC change. Selected case studies illustrate the range of approaches currently being used and insights emerging from them. They also emphasize coupled social–ecological systems: humans respond to

Table 9.2.
Strengths and weaknesses of different approaches to landscape scenarios.

Scenario approach	Strengths	Weaknesses
Projective	• Empirically based • Quantitatively rigorous • Best over shorter time intervals • Useful to ask "what if past or current uses continue into the future?"	• Assumes stationarity • Past rates and relationships may have little to do with the future • Conservative; difficult to "think outside the box"
Prospective	• Can incorporates many viewpoints • Preferred when uncertainty is high and uncontrollable • Useful to as, "what are the future consequences of different decisions or policies?"	• May get so complicated that models are less useful • Time consuming, resource intensive to do well

cues from the physical environment and from sociocultural contexts (Riebsame et al. 1994; Turner and Robbins 2008). Given the extensive influence of human land use on landscape structure and function, it is folly to consider the future of any landscape in isolation from the humans that inhabit or manage it.

National Scenarios

In many countries, there is tremendous interest in assessing future scenarios of climate and land-cover change because of the need to consider different strategies that may affect greenhouse gas fluxes and carbon sequestration, to plan for needed infrastructure, and anticipate where future resource demands are likely to compete. Two major programs in the US have developed prospective scenarios for future land cover in association with IPCC scenarios. As part of the US Geological Survey program to assess carbon sequestration and greenhouse gas fluxes for US ecosystems, researchers developed methods for downscaling (to 250-m resolution) global LULC change projections from the IPCC third Assessment Special Report on Emission Scenarios (SRES) to ecoregions of the US (Sleeter et al. 2012). They developed an approach for spatial downscaling that first determined the amount of land that would be dedicated to different uses, and then determined how the land uses would be allocated spatially in a given landscape. Drivers of LULC change included globalization, regulation, technological development and innovation, population growth, economic development environmental protections, energy consumption, and social attitudes. From national demand, ecoregions were assigned different LULC conversions, and a patch-based spatial allocation model was used to position the LULC conversions within each ecoregion. Expert knowledge was used to translate socioeconomic scenarios into equations that would simulate change. The resulting scenarios offered contrasting patterns, as shown for forest and grassland/shrubland covers (Fig. 9.8; Sleeter et al. 2012). This study was the first to regionalize future changes in the US such that they were consistent with global assessments.

The US Environmental Protection Agency (2009) developed a complementary set of housing density scenarios that were also based on IPCC SRES storylines but used demographic models to project housing allocation at the county level throughout the US. Called the Integrated Climate and Land-use Scenarios (ICLUS; http://www.epa.gov/ncea/global/iclus/), the models projected the area of urban, suburban, and exurban housing density and the land-cover types (forest, shrubland, grassland, cropland, and wetland) that would be converted to built areas through 2100. County-level population estimates were distributed to 1-ha resolution housing density by a spatial allocation model, and results were output at a decadal scale. Among scenarios, the models projected between 60 % (for B1) and 164 % (for A2) increases in urban and suburban land areas by 2050. The scenarios were also linked with indicators of ecological effects, such as the area of impervious surface, so that differences in effects among scenarios could be compared. The scenarios exercise found that many watersheds could experience future stress because impervious cover would increase to at least 5 % of the watershed (US EPA 2009), which could lead to increased runoff and nutrient delivery to surface waters.

Regional Scenarios

Spatial models that compare alternative future scenarios of landscape change can help researchers and managers visualize and evaluate alternative choices for a particular region, and a nice example is provided by studies in the agricultural Midwest, USA (Santelmann et al. 2004). A normative scenario exercise was designed to help determine what should be done within the region. The Midwest was subjected to extensive land conversion, largely to intensive agriculture, starting in the mid-1800s (Curtis 1959; Baker et al. 1996). Much of the region is now in row crops, primarily a rotation of corn and soybeans. A variety of ecological problems have ensued, including fragmentation of remaining natural habitat, loss of soil carbon, and deterioration of water quality (e.g., Curtis 1959; Burgess and Sharpe 1981; Carpenter et al. 2007). Land-use patterns that minimize deleterious effects on terrestrial and aquatic ecosystems while maintaining agricultural productivity in the Midwest are desired.

Three alternative future scenarios were designed for two agricultural watersheds in Iowa, USA, to represent their potential landscape composition ~25 years into the future (Santelmann et al. 2004). In consultation with a range of disciplinary experts, a team of landscape architects led the development of the scenarios.

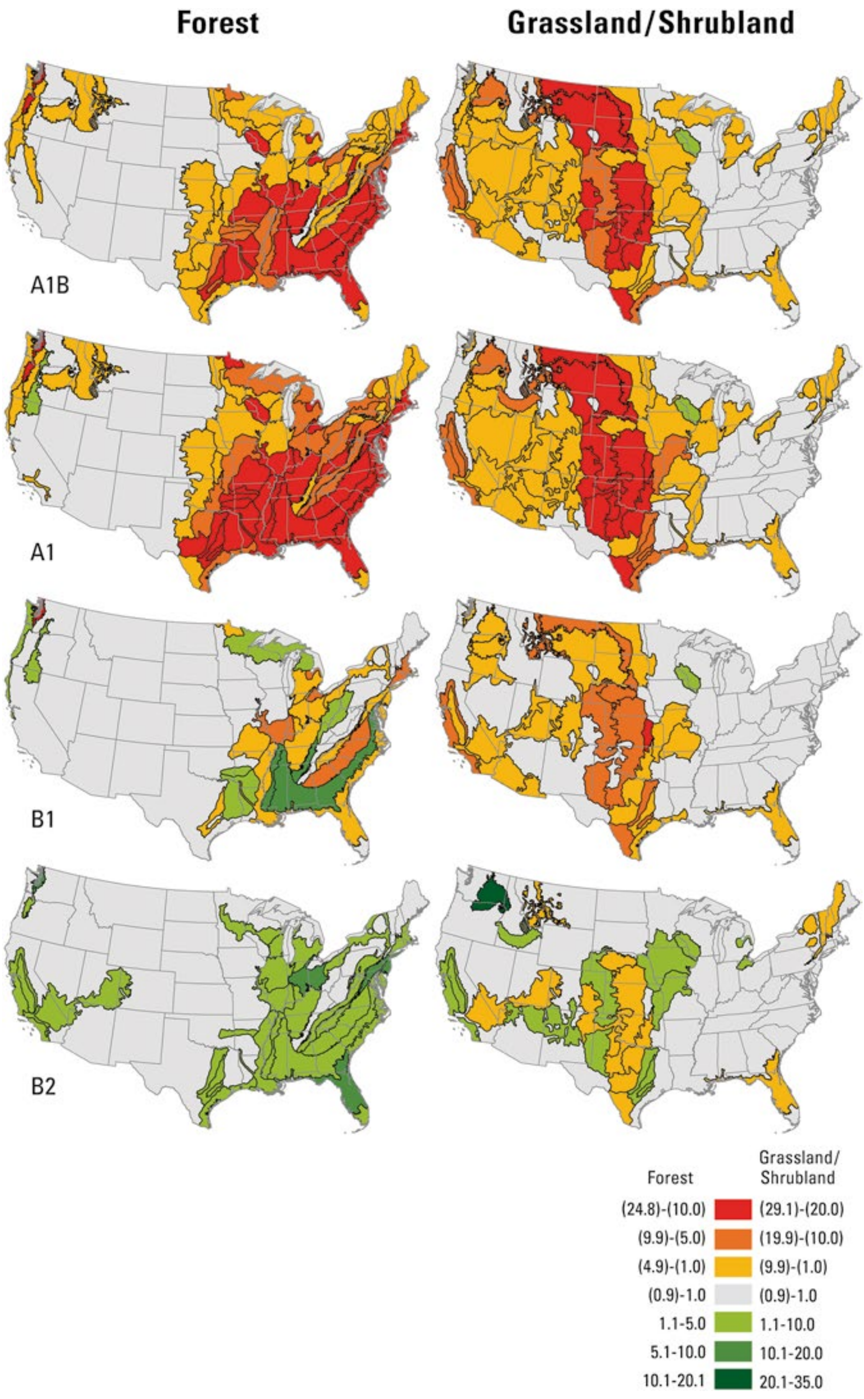


FIGURE 9.8.

Projected change in forest and grassland cover in the conterminous USA from 2000 to 2100 under four IPCC fourth assessment emissions scenarios. Units are the percent of Level III ecoregions that change.

REPRINTED WITH PERMISSION FROM SLEETER ET AL. (2012).

Scenarios included (1) continuation of present trends in which food production and economic profit receive highest priority, (2) an effort to preserve biodiversity and improve water quality using conventional methods, and (3) incorporation of a greater range of innovative agricultural practices coupled with effort to preserve and restore native biodiversity and improve water quality (Fig. 9.9). To help people understand the scenarios, visualizations were developed for each (Fig. 9.10). The future landscapes were linked with a constellation of different modeling approaches to explore consequences for water quality; aquatic, wetland, and terrestrial biodiversity; and economic impact on farmers (Santelmann et al. 2004). In addition, farm planning was addressed to incorporate input from local farmers and decision-makers and to explore how socioeconomic constraints translated into land-use and management decisions. The long-term significance of this approach rests in its ability to inform landowners and policy-makers (e.g., those crafting legislation that affects agricultural policy) about ecological and social effects of land-use and management in agricultural landscapes like those in the Midwest. Use of a wide array of ecological consequences allowed for a comprehensive evaluation of the scenarios.

Another regional example, this time illustrating a prospective scenarios approach, comes from the Willamette River Basin, Oregon, located in the Pacific Northwest region of the USA. This example also contrasts participatory and expert approaches to scenario development (Baker et al. 2004; Hulse et al. 2009). First, LULC changes in the basin were generated by producing maps of the basin from 1850 to 1990; these maps provided the baseline conditions. Next, a 30-month long process of citizen involvement was undertaken to generate three alternative scenarios for 2050. These three participatory scenarios were alternative 2050 endpoints (i.e., single maps rather than alternative trajectories), and they contrasted goals of achieving short-term wealth vs. long-term ecological function, as well as an intermediate that was similar to business as usual. A quantitative landscape model (Evoland) based on expert opinion and rule-based methods was also developed. Evoland represented “agents” (who have decision-making authority over parcels of land), the landscape (which is changed as decisions are made), and policies (which guide and constrain decisions). The model was probabilistic, and 75 replicates were simulated for two of the citizen-generated scenarios (Development 2050 and Conservation 2050, Fig. 9.11.) In contrast to the single map generated for each scenario by the stakeholders, the expert approach using Evoland identified multiple possible outcomes for some parts of the landscape (white areas in Fig. 9.11). By identifying areas of future uncertainty, the quantitative landscape model located specific places where strategic planning could be focused to nudge the landscape toward a more desirable state. Interestingly Evoland simulations also predicted that more of the landscape would change land-cover state compared to the participatory scenarios, suggesting that people may be somewhat conservative in envisioning future change.

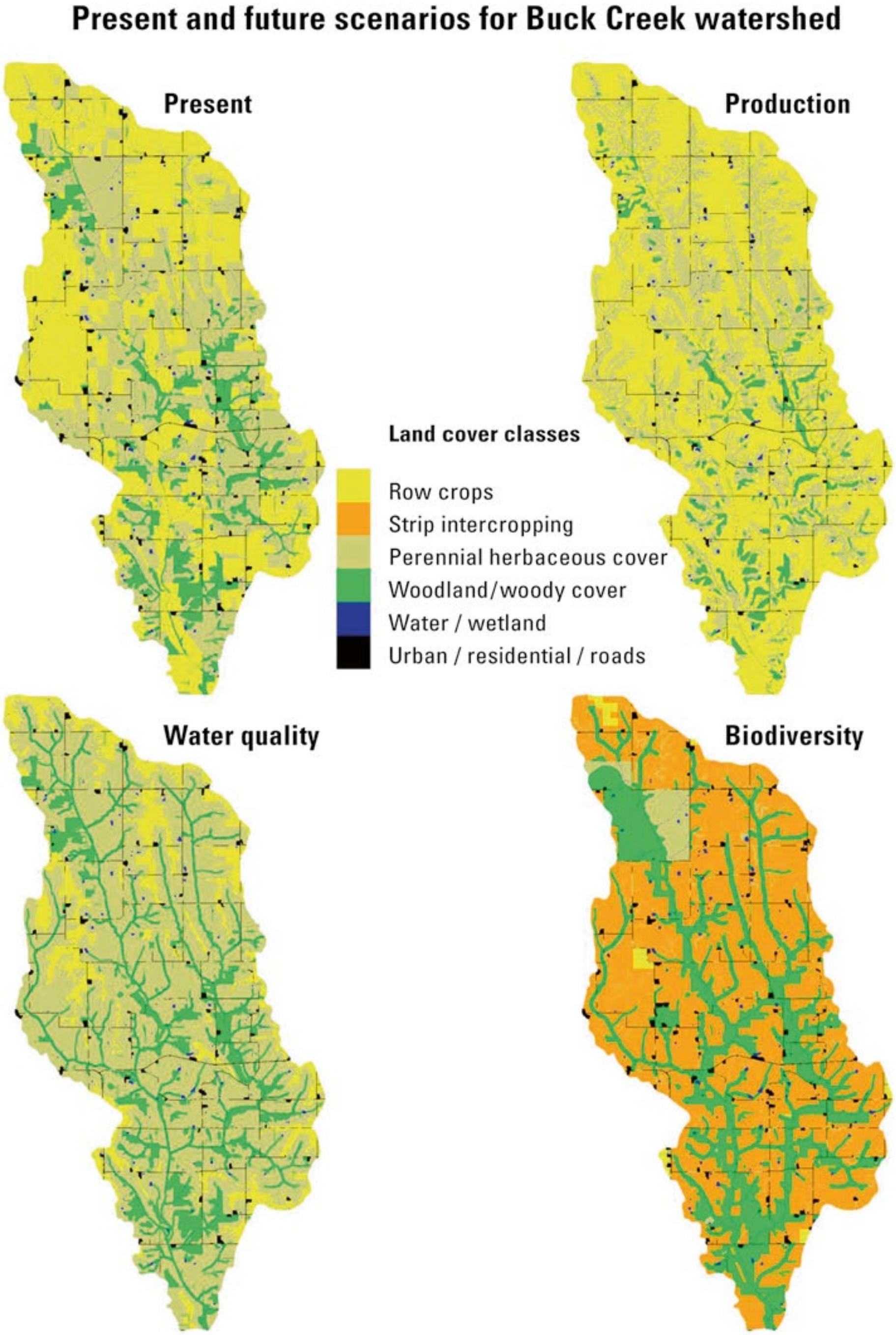


FIGURE 9.9.

Maps of alternative future scenarios for a watershed in Iowa, USA. Maps show present landscape patterns (*top left*) and three scenarios that emphasize agricultural production (*top right*), agricultural management innovations to improve water quality (*lower left*), and efforts to preserve biodiversity (*bottom right*).

REPRINTED WITH PERMISSION FROM SANTELMANN ET AL. (2004).

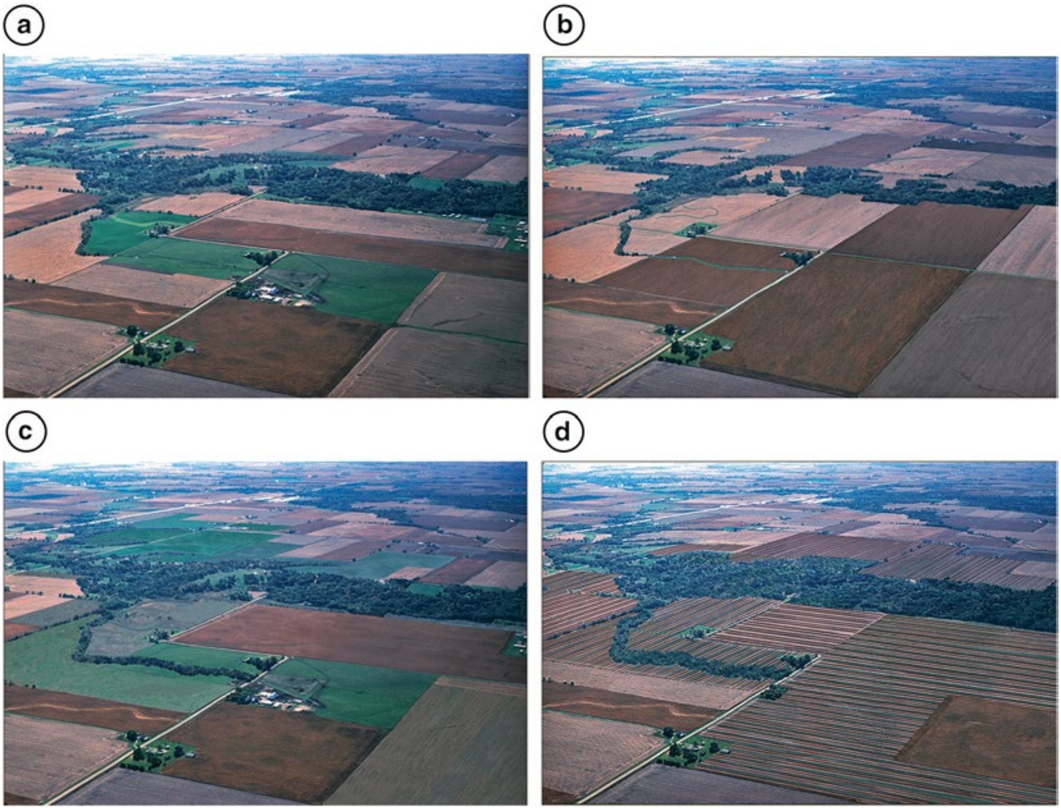


FIGURE 9.10.
Alternative future scenarios for a watershed in Iowa, USA. (**a**) Present conditions. (**b**) Continuation of current trends. (**c**) Effort to preserve biodiversity and improve water quality using conventional methods. (**d**) Incorporation of more innovative agricultural techniques to restore biodiversity and improve water quality.

COURTESY OF JOAN NASSAUER.

Lastly, a study of the Mallee region, Lower Murray River in southeastern Australia illustrates how different types of scenario can be combined (Bryan et al. 2011). The Murray originates in the Australian Alps and flows through this is semiarid region dominated by agriculture en route to the Southern Ocean. Bryan and colleagues combined four future climate scenarios with four spatial policy options for natural resource management in a factorial design. Climate scenarios came from the IPCC. Spatial policy options included random allocation; selection based on minimizing economic cost (cheapest); select spatial units based on maximizing environmental benefits (best), including biodiversity, reduced wind erosion and salinization; and selection of spatial units that were most cost-effective for meeting multiple environmental objectives (most cost-effective). Impacts from each combination ($n = 16$) were calculated for a range of environmental,

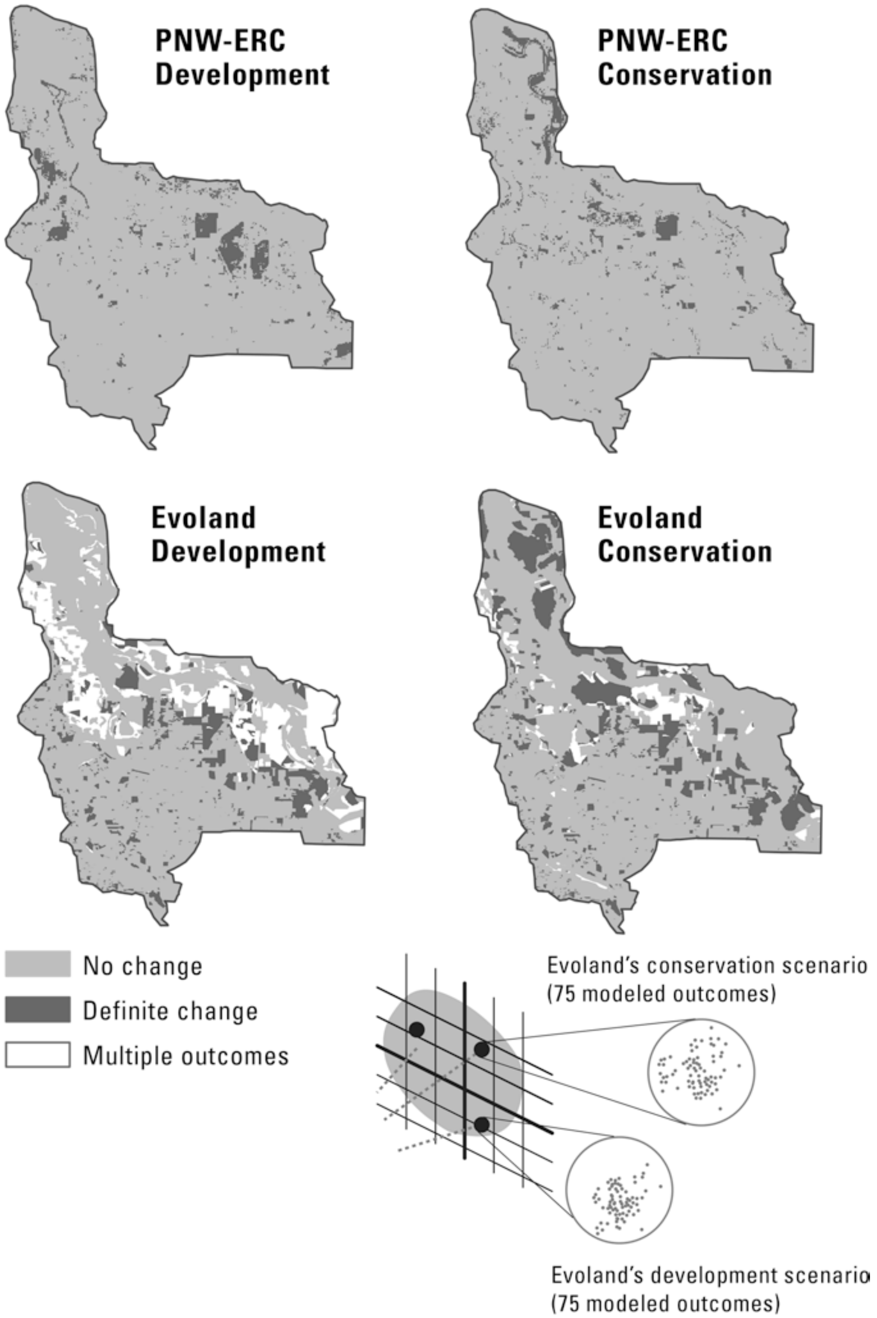


Figure 9.11.
Alternative future landscape trajectories for the Willamette River Basin, Oregon, from 2000 to 2050 that emphasize either development or conservation goals. *Upper maps* show stakeholder-driven projections. *Lower maps* result from a simulation model, Evoland. Locations that do not change are in *light gray*, those that definitely change are in *dark gray*. Areas in *white* may have multiple outcomes, which only occurs in Evoland.

Reprinted with permission from Hulse et al. 2009.

economic, and social indicators. Results revealed interesting interactions in which the land-use outcomes differed substantially under different future climates (Bryan et al. 2011). Most importantly, the study demonstrated that environmental goals could be achieved more cost effectively through spatial planning. In other words, paying attention to the spatial allocation of land uses could lead to "win–win" outcomes.

As these examples demonstrate, exploring alternative future scenarios is proving to be extremely useful in landscape ecology. Quantitative landscape scenarios can identify the range of conditions that produce either desirable or undesirable outcomes, and if a desirable condition is identified, scenarios can help determine how to achieve them. In all cases, it is important to know thy landscape, know thy patches, and know thy drivers. Outcomes depend on initial conditions, and a small number of sites may have been "keystones" that have disproportionate influence on outcomes. Among drivers, it is especially important to distinguish the influence of external factors versus factors internal to the landscape (e.g., policy options, agent action) that drive LULC change.

Many important questions in applied landscape ecology could benefit from a scenarios-based approach. For example, scenarios may help to determine: Are there LULC patterns, or designs, that minimize deleterious effects? How many different LULC pathways may arrive at the same endpoint? Under what conditions can LULC patterns amplify or dampen the effects of other drivers, such as climate? How much can be gained by manipulating LULC patterns within a landscape? There are many opportunities for improving quantitative landscape scenarios, as these methods remain much in development. Improvements in algorithms are needed to blend quantitative and qualitative information in scenarios, to visualize and summarize the voluminous data that result from scenario analyses, to capture uncertainty in spatial data and temporal variation, and to better develop the functional consequences of LULC change.

Land Use: Synthesis

The question about land use is not whether we should or should not use land, but rather how we can best use the land (Turner et al. 1998a). The answer is not straightforward; there are no "cook book" approaches for identifying optimal arrangements, no guarantees that what works in one social–ecological setting will work in another. Landscape ecology contributes principles and techniques for considering how to arrange human structures spatially and identify potential ecological implications of alternative arrangements. Although land use is one driver that is controllable (at least, in theory), it has also been called a "wicked problem" because of the complexities involved. Santelmann et al. (2004) identified five conditions that must be met for practical application of ecological principles in land-use decision-making:

1. Decision-makers must understand the need and share the goal.
2. Abstract principles must be translated into specific land-use decisions.
3. Responsibility for associated costs and labor (which tend to occur up front and are specific to place) must be assigned and accepted (i.e., made economically feasible).
4. Benefits (which tend to be realized in the longer term and diffuse in space) must be understood and shown to have value.
5. Practices must be culturally acceptable (this includes respect for the rights of property owners).

To date, studies of LULC change point to several interesting observations. One is that initial conditions may strongly shape the future—existing landscape patterns have a strong influence on future conditions. Another is disproportionality, as in many examples of LULC change, a comparatively small number of pivotal parcels may have surprisingly large effects on outcomes, either positive or negative. Understanding how current conditions constrain future options and identifying “keystone elements” in the landscape seem especially important.

Many research frontiers remain within land-change science. Deciding how best to visualize and analyze scenarios, given the multiple ways to characterize landscape patterns, changes and effects, can be overwhelming. Land-use changes are often not considered jointly with other processes that alter land cover, such as natural disturbances, and spatially explicit scenarios still need better ways to incorporate surprise into modeled futures. From a practical standpoint, there is much to be learned regarding how much the decisions about how much and where to arrange different LULC elements affect the ability to reach some desirable goal, and the degree to which landscape patterns may mitigate or amplify the effects of other drivers.

Interdisciplinary studies are often complex (e.g., Turner and Carpenter 1999; Naiman 1999; Wear 1999; Pickett et al. 1999), but there should be strong encouragement to develop the integration required for more effective modeling of social–ecological systems. Riebsame et al. (1994) made several suggestions for improved land-use/land-cover modeling. These include: (1) improved methods and approaches for integrating sociocultural factors, as social driving forces must be coupled with their ecological effects and feedbacks to society; (2) modeling interactions among multiple resources, not just one or two; (3) modeling cumulative effects, particularly when a threshold response (e.g., sudden disconnection of habitat) may be likely; (4) dealing with surprise—that is, unusual conditions, rapid change, and potential surprises that may come from the environment or society.

Although these were written 20 years ago and progress has been substantial, especially with respect to representing human decision-making in land-change models (see Brown et al. 2013 and National Research Council 2013), these needs remain timely. Riebsame et al. (1994) also wrote, “Our limited ability to simulate realistic land-use patterns is not just a modeling problem, but a reflection of the real world.” As in the first edition of this book, we concur with this evaluation and suggest that this area of applied research presents a compelling challenge to landscape ecology that will persist for the coming years.

ECOSYSTEM SERVICES AND LANDSCAPE SUSTAINABILITY

A key reason for considering future climate and land-use change in landscape ecology, and for using scenarios to explore plausible future conditions, is the shared goal of sustaining the structure and function of landscapes for decades to come. One way to approach this goal is by considering *ecosystem services*, or the benefits that people obtain from ecosystems, which were well articulated in a classic book by Gretchen Daily (Daily 1997). Since then, and largely because of the international Millennium Ecosystem Assessment (Millennium Ecosystem Assessment 2005), ecosystem services have become a nexus for environmental research and policy. Ecosystem services are increasingly included in policy decisions related to sustainability, and government programs in the US and Europe focus on their management and sustainability (e.g., Schröter et al. 2005; Gaston et al. 2013). Understanding how the resilience of landscapes and their ability to sustain ecosystem services in the face of changing drivers, such as climate and land use, is an important goal. *Resilience* refers to the capacity of a system to tolerate disturbance without shifting to a qualitatively different state that is controlled by a different set of processes (Resilience Alliance 2012). In other words, resilience is the ability of a system to retain its function, structure, identity, and feedbacks in the face of disturbance and environmental change (Walker et al. 2004).

There is no generally accepted definition of landscape sustainability. *Sustainability* refers to use of the environment and resources to meet current needs without compromising the ability of a system to provide for future generations. Here, we emphasize the capacity of landscapes to deliver desired ecosystem services in the face of human land use and a fluctuating environment, now and in the future (Chapin et al. 2009b), which we call *landscape sustainability*. This aligns fairly well with use of the term by others. For example, landscape sustainability was described as a desirable trajectory and condition that scientists can document, people can perceive, and nature can exist within (Musacchio 2009). However, the concept can be applied in subtly different ways depending on whether it is the landscape itself that is emphasized or its influence on other goods or services. Wiens (2013) distinguished between using landscape sustainability for the degree to which the patterns and processes that characterize a landscape will persist into the future, versus how landscape features affect the sustainability of things that matter to people or to organisms. As Wiens noted, the second definition is strongly dependent on the first. Because of the strong relationships between landscape heterogeneity and ecosystem structure and function, spatial heterogeneity does affect ecosystem services, and landscape ecology can make key contributions to sustainability science (e.g., Musacchio 2009; Cumming 2011; Turner et al. 2013).

Ecosystem services are commonly grouped into broad categories (provisioning, regulating, cultural, and supporting) that reflect different kinds of benefits derived from nature (Table 9.3; Millenium Ecosystem Assessment 2005). These services are provided by spatially heterogeneous landscapes and seascapes. Some services can be measured directly, for example, crop yield and timber harvest, whereas others are more difficult to quantify. Many ecosystem services are assessed using biophysical indicators, often based on empirical relationships or simulation models. The Natural Capital Project (www.naturalcoapitalproject.org) developed a software

TABLE 9.3.
ECOSYSTEM SERVICE CATEGORIES, AS DEFINED BY THE MILLENIUM ECOSYSTEM ASSESSMENT (2005).

Category	Definition	Examples
Provisioning services	Products people obtain from ecosystem and use directly	Food, fuel, wood, fiber, fresh water, genetic resources
Regulating services	Benefits people obtain from the regulation of ecosystem processes	Air quality maintenance, climate regulation, erosion control, regulation of human diseases, water purification, pollination, pest control
Cultural services	Nonmaterial benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, etc.	Esthetic experience, religious value, education, recreation, wildlife viewing
Supporting services (i.e., natural capital)	Services that provide the foundation for all other ecosystem services; because of this, they are sometimes not considered an ecosystem service per se because they do not benefit people directly	Primary production, soil formation, biogeochemical cycling, oxygen production

THESE BENEFITS TO PEOPLE FROM NATURE ARE KEY CONSTITUENTS OF HUMAN WELL-BEING AND ECOLOGICAL SUSTAINABILITY AT LOCAL, REGIONAL, AND GLOBAL SCALES, YET THEY ARE OFTEN UNDERAPPRECIATED.

system, called InVEST, that is widely used to quantify ecosystem services across land- and seascapes and explore consequences of different management alternatives on the economy, the environment, and human well-being.

Assessing, projecting, and managing the flows of ecosystem services across spatially heterogeneous landscapes are important topics in sustainability science (e.g., Carpenter et al. 2009; Turner et al. 2013; Wiens 2013). However, the spatial ecology of ecosystem services is not well understood. We do not attempt a comprehensive review of the ecosystem services literature, nor do we address the economic valuation of ecosystem services; we refer readers to existing literature [e.g., Kremen 2005; Kremen and Ostfeld 2005; Daily and Matson 2008 and the rest of special feature on ecosystem services in PROCEEDINGS OF THE NATIONAL ACADEMY OF SCIENCES; Daily et al. 2009]. Rather, we emphasize spatial patterns and dynamics of ecosystem services in the context of landscape sustainability. We begin by providing illustrative examples of how landscape heterogeneity influences a few different ecosystem services, then discuss spatial relationships among multiple ecosystem services, how biodiversity is treated in ecosystem services assessments, and priorities for research.

Landscape Heterogeneity and Ecosystem Services

Hydrologic ecosystem services are freshwater benefits to people generated by terrestrial ecosystems, including freshwater supply, water quality, flood mitigation, and cultural services related to freshwater (Brauman et al. 2007). Freshwater services are of particular concern in agricultural and urban landscapes, as they are especially sensitive to landscape changes associated with the amount and pattern of impervious surfaces, such as roofs, roads and parking lots; nutrient additions, such as fertilizer application; and water extraction, as for irrigation (Kepner et al. 2012). Urbanization and agricultural intensification can alter ecohydrological processes and introduce contaminants (DeFries and Eshleman 2004; Brauman et al. 2007; Kepner et al. 2012). Intensive agriculture accompanied by excessive nutrient inputs from commercial fertilizer and manure applications can trigger eutrophication and groundwater contamination. Growing urban impervious surface can increase “flashiness” of runoff from heavy rainfall events, resulting in more frequent and severe floods. Even in less-developed landscapes, excess water extraction for hydrologic fracturing associated with fossil fuel extraction can alter the water table and stream flows. These landscape changes may interact with other drivers such as changing climate to challenge the sustainability of hydrologic ecosystem services.

In the Yahara Watershed, Wisconsin, USA, four different ecosystem services related to water quality and quantity were quantified using biophysical indicators and mapped at 30-m resolution for the entire watershed for a single year (Qiu and Turner 2013). The hydrologic services were provided by different parts of the landscape, with some locations contributing to groundwater recharge, others to flood mitigation, and still others to surface and groundwater quality. The study showed that management to sustain the portfolio of freshwater services in the landscape will not be simple (Qiu and Turner 2013).

Pollination is an ecosystem service that is critical for food production. Pollination is especially sensitive to landscape composition and configuration, in part because it is often provided by mobile organisms (Lundberg and Moberg 2003). About one-third of crop production depends on animal pollinators, and 60–90 % of plant species rely on animals for pollination (Kremen et al. 2007). Sustaining local pollination services requires a landscape that provides the foraging resources needed for the pollinators at spatial scales aligned with their foraging ranges and dispersal distances. For example, Priess et al. (2007) found a strong influence of the extent and location of deforestation on pollination of coffee in Central Sulawesi, Indonesia, and identified a critical role for remnants of native forest. In coffee plantations, pollinator diversity and fruit set of coffee decline with increasing distance to intact forest. Thus, pollination services decline as deforestation progresses and remnant forests become fewer and more isolated. When the mean distance between coffee plantations and forest increases to 150 m, coffee yield and pollination services are 95 % and 69 %, respectively, of their values right at the forest edge. As habitat loss and fragmentation continue and this mean distance increases to 400 m, these percentages for yield and pollination drop to 85 % and 48 %, respectively (Priess et al. 2007). The monetary value of the pollination services provided by forests in the study area was estimated €46 ha^{-1} (Priess et al. 2007). Thus, landscape pattern matters a lot for pollinations services and coffee production, and remnant forests play a critical role in these human-dominated tropical landscapes.

Forest fragments are important for many ecosystem services in agricultural landscapes besides pollination. In an agricultural landscape in Quebec, Canada, a study of six different ecosystem services in relation to forest fragments reported significant effects of distance-from-forest, fragment isolation and fragment size on crop production, insect pest regulation, and decomposition (Mitchell et al. 2014). Structurally complex agricultural landscapes generally tend to enhance local biodiversity, and landscape heterogeneity may help offset some consequences of local high-intensity management (Tscharntke et al. 2005). Having a mixture of natural and seminatural cover types in the agricultural landscape can enhance resilience by maintaining high diversity of different functional groups, and patches of native vegetation also may enhance dispersal of beneficial organisms by providing stepping stones across the landscape (Tscharntke et al. 2005). Indeed, some authors (e.g., Swift et al. 2004) have suggested that promoting regional land-use diversity is the major opportunity for maintaining ecosystem services and biodiversity outside of conservation areas.

Recent decades have seen a push for increasing use of renewable energy, including bioenergy, in local, regional, and national energy budgets. Different kinds of biomass, including corn, herbaceous vegetation (e.g., switchgrass, *Panicum virgatum*), and short-rotation woody crops (e.g., *Populus* species), have been promoted as renewable sources of energy feedstocks and thus another potential ecosystem service to be supplied from a landscape. Corn is the dominant biofuel crop in North America, and acreage in corn has been increasing. In the US, the 2007 Energy Independence and Security Act called for up to 15 billion gallons per year of corn-based ethanol, most of which is made from corn grain, by 2015. Because ecosystem disservices are associated with intensive row-crop agriculture, the potential for perennial cropping systems to produce biomass for bioenergy has been explored, in part because these are expected to produce net benefits for grassland wildlife (Fargione et al. 2009; Fletcher et al. 2010; Meehan et al. 2010). Landscape ecology can contribute to the bioenergy discussion by exploring the consequences of alternative amounts and arrangements of different bioenergy crops on energy production and other services. For example, Dale et al. (2011) suggest a variety of specific roles for landscape ecology at the nexus of land use, energy development, and climate change. Included among their suggestions are the need for case studies that use relevant indicators across the full life cycle of energy production, models that allow the consequences of alternative landscape designs to be evaluated, and identification of the appropriate scales for assessing landscape sustainability.

Landscape connectivity is a key spatial attribute that may influence the supply of ecosystem services because lateral movements of organisms and matter are components of many ecosystem services. Mitchell et al. (2013) provided a semiquantitative review of the landscape connectivity–ecosystem services literature, which we briefly summarize here. Landscape connectivity is expected to influence services such as pollination, pest regulation, seed dispersal, and disease regulation, which depend on the movement of organisms across landscapes. Whether connectivity of a particular habitat is associated with increased or decreased service supply depends on the service. Increased connectivity of crop fields may facilitate movement of crop pests across the landscape, whereas increased connectivity of seminatural habitats may facilitate movement of natural enemies that help to regulate crop pests. However, such relationships may be surprisingly complex, as when landscape complexity alters the interactions among natural enemies. For example, in experimental plots in South Korea, interactions among birds, flying insects, and ground-dwelling arthropods varied with landscape complexity and led to different levels of pest control (Martin et al. 2013).

Landscape connectivity is also expected to influence services that relate to movement of matter, such as fresh water provision, regulation of air and water quality, erosion, and mitigation of natural hazards. However, assessment of the published literature revealed that most studies did not provide empirical evidence that ecosystem service provisioning was altered as landscape connectivity changes (Mitchell et al. 2014). Functional connectivity (vs. structural connectivity) was generally unmeasured, with only three studies, all involving birds and seed dispersal services, measuring actual animal movement across landscapes and relating movements to ecosystem services. Pollination was well studied, with many studies linking the presence and pattern of natural ecosystems to pollination (Mitchell et al. 2013). Overall, the review found that the view that landscape connectivity should affect ecosystem services was widely held, but there was surprisingly little empirical evidence or well-developed theory. Thus, there are a number of key opportunities for future research (see Table 1 in Mitchell et al. 2013).

Interactions Among Ecosystem Services

Most landscapes produce multiple services—for example, they may produce food or wood products while also providing drinking water and recreational opportunities. The degree to which different ecosystem services are spatially concordant (produced at the same locations in a given landscape) or spatially disjunct (with different locations producing different services) has not been widely studied in different kinds of landscape (but see Naidoo et al. 2008; Nelson et al. 2009). Some sets of ecosystem services—called *bundles*—always appear together across space or time (Raudsepp-Hearne et al. 2010). However, attempts to maximize the production of one ecosystem service or bundle often results in substantial declines in other ecosystem services, which argues for the need to understand the relationships among multiple services and the mechanisms underpinning these relationships (Bennett et al. 2009).

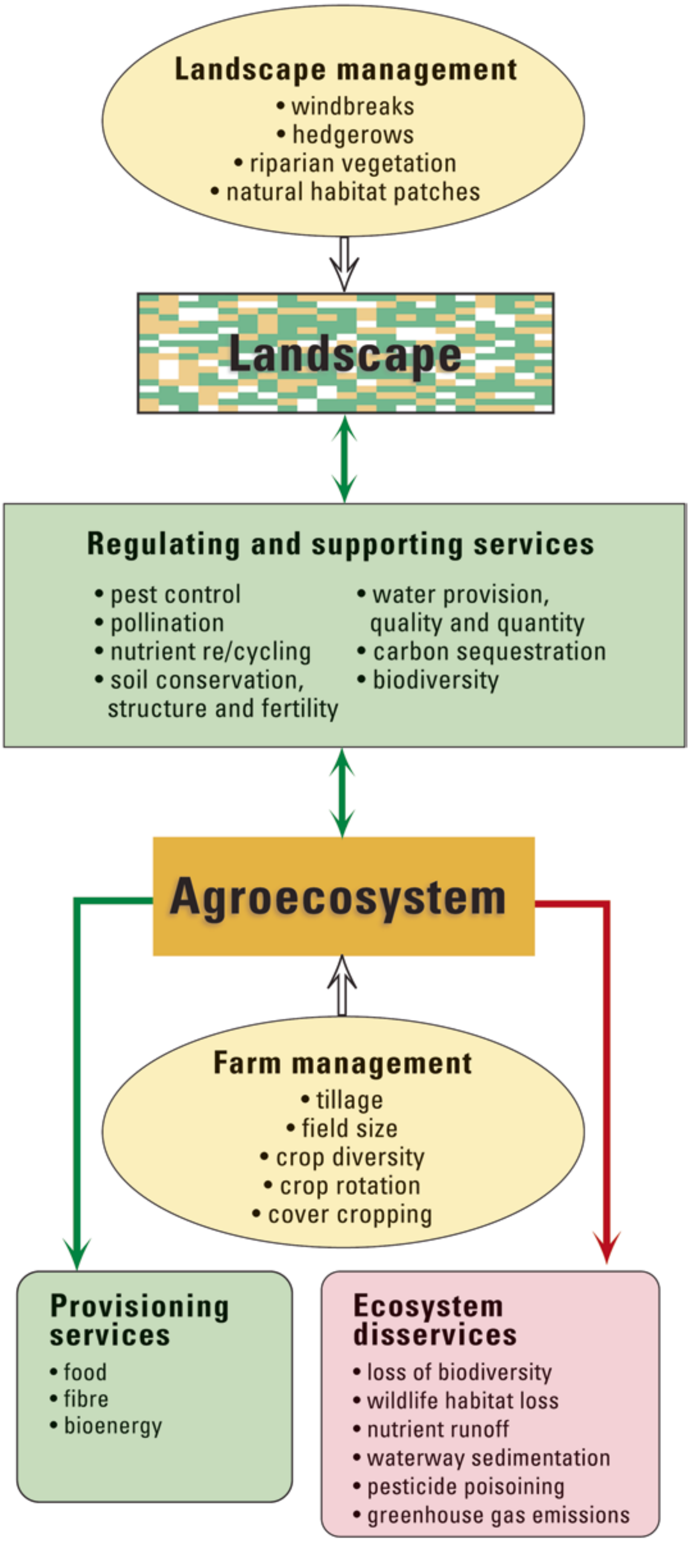
Synergies arise when multiple services are enhanced simultaneously (Bennett et al. 2009), and *trade-offs* occur when the provision of one service is reduced as a consequence of increased use of another (Rodriguez et al. 2006). Thus, synergies occur with positive correlations among ecosystem services, and trade-offs occur with negative correlations. Agricultural landscapes have received much attention because there are often trade-offs between crop production and other services; depending on management, agriculture may produce disservices, such as habitat loss, nutrient and sediment runoff, pesticide poisoning of nontarget species, and greenhouse gas emissions (Fig. 9.12; Power 2010). Synergies and trade-offs may vary with scale, but a distinct trade-off at the field scale may obscure synergies at other scales.

Agricultural landscapes provide opportunities for studying interactions among competing ecosystem services. In the Yahara Watershed study mentioned earlier, Qiu and Turner (2013) studied the production, spatial distribution, and interactions among ten provisioning, regulating, and cultural ecosystem services. In this agricultural landscape, spatial patterns of high supply for multiple ecosystem services often were not spatially concordant; locations where six or more services were produced at high levels (upper 20th percentile) occupied only 3.3 % of the landscape and often coincided with nature preserves, parks, and riparian zones. Half of the landscape produced high values of one or no ecosystem service; these locations were primarily croplands or developed lands. The study identified three

Figure 9.12.

Landscape and farm management affect the flow of ecosystem services and disservices in an agricultural landscape.

Adapted from Power (2010).



distinct groups of ecosystem services that revealed synergies and trade-offs among the ten services (Qiu and Turner 2013). Most relationships among ecosystem services were synergies (i.e., positive correlations), but trade-offs occurred between crop production and water quality. The spatial patterns of synergies and trade-offs among ecosystem services were complex (Fig. 9.13). Different areas of the landscape supplied different suites of ecosystem services. Hotspots were rare on the landscape, indicating the difficulty of obtaining high supplies of multiple services from the same parcel in a landscape dominated by agriculture and urban land. However, hotspots could be very important because areas of high supply of multiple ecosystems services may coincide with greater species and functional diversity (Lavorel et al. 2011). The spatial heterogeneity of different ecosystem services and their interactions indicate that sustainability of ecosystem service production requires regional-scale management that accounts for the geographic position and spatial distribution of services (Qiu and Turner 2013). It is not possible to obtain high values of all services from the same parcel of land, and so, for example,

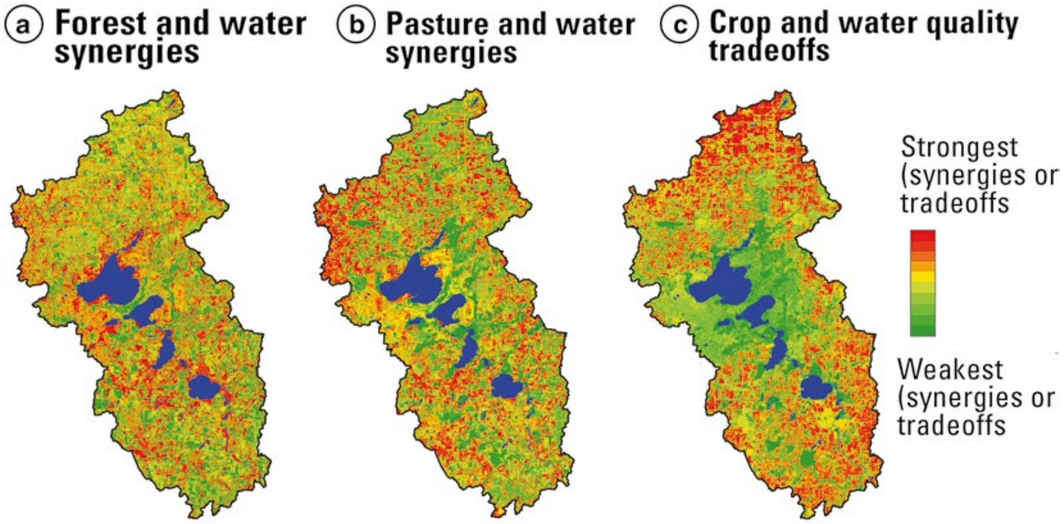


Figure 9.13.

Spatial interactions among ecosystem services in the Yahara Watershed of southern Wisconsin, USA. Mapped values are factor scores that represent synergies and trade-offs among ecosystem services: (**a**) Factor 1, forest and water synergies. *Red* represents areas where carbon storage, surface water quality, forest recreation, and soil retention are high, whereas *green* represents areas where all these services are low. (**b**) Factor 2, pasture and water synergies. *Red* represents locations where pasture production, flood regulation, and freshwater supply are all high, whereas *green* represents locations where all these services are low. (**c**) Factor 3, crop and water quality trade-offs. *Red* represents where crop production is high, and surface and ground water quality are both low.

From Qiu and Turner (2013).

locations producing food may need to be complemented by other locations that can store carbon.

Anticipating future production and delivery of multiple ecosystem services as various drivers change is a critical component of landscape sustainability. Interdisciplinary research teams are beginning to address this by modeling alternative future landscape conditions and their potential consequences for multiple ecosystem services. For example, increased urban land cover was modeled for Britain, UK, based on an anticipated 16 % increase in human population by 2031 (Eigenbrod et al. 2011b). Spatially, the increased urbanization bracketed alternative arrangements: a "densification" scenario that minimized the expansion of urban areas, and a "sprawl" scenario that expanded urban land cover following current suburban patterns. Consequences were modeled for three different ecosystem services: flood mitigation, agricultural production, and carbon storage. These services responded differently to each scenario. The densification scenario led to 1.7 million people living within 1 km of rivers with at least 10 % increases in peak flows, but the sprawl scenario had little effect on flooding. In contrast, losses of agricultural production and carbon storage were more than three times as high in the sprawl scenario as in the densification scenario. This study underscores the challenge of managing the landscape to provide multiple services—the optimal arrangement for one ecosystem service may be very different from the optimal arrangement for another. This also points to the need for managing larger areas for multiple ecosystem services, as different parts of the landscape will produce high values of different ecosystem services (Qiu and Turner 2013). Bundles of services may be optimized together, but larger areas will be needed to sustain a diverse suite of multiple services.

Ecosystem Services and Biodiversity

Ecosystem services and biodiversity are both of interest in landscape ecology and management, but integrating these two has been challenging. Inclusion of biodiversity in assessments of ecosystem services is inconsistent, and indicators of biodiversity and ecosystem services seldom follow a common monitoring scheme (Feld et al. 2009). Following what Mace et al. (2012)) refer to as a "conservation perspective," biodiversity is considered in parallel with other services, and conservation often ends up as a trade-off. For example, species richness and conservation value is usually low in row crops, but crop yields may be high, resulting in a trade-off between biodiversity and food production at the field scale (Power 2010; Fletcher et al. 2010). Globally, areas selected for conservation of biodiversity often do not coincide with areas producing high values of multiple ecosystem services such as carbon storage, carbon sequestration, and water provision (Naidoo et al. 2008). By often focusing on species, the "conservation perspective" may ignore the role of biodiversity as a supporting service, providing the underpinning ecosystem processes.

Confusion about how to consider biodiversity and ecosystem services jointly has also ensued because biodiversity can be a regulator of important ecosystem services as well as a final ecosystem service in its own right (Mace et al. 2012). Genetic and species diversity can contribute directly to some ecosystem services, as when particular strains of crops, biofuels, or livestock are selected to enhance production. But, biodiversity can also directly provide important cultural ecosystem services, as when recreational experiences are enhanced by the presence of watchable wildlife or flowering plants. Mace et al. (2012)) advocate for recognizing that diversity per se contributes directly to delivery of some services but not others, and that biodiversity likely contributes more to regulating and cultural services and less to provisioning services. Across Europe, habitats that were in conservation status supplied more regulating services, provided more water, and higher recreation potential than other habitats (Maes et al. 2012).

Understanding the sensitivity of different ecosystem services to the types and levels of biodiversity in different landscapes, and how these relationships vary with scale, remains limited. Mace et al. (2012) note that effective ecosystem management requires identifying and analyzing ways to optimize ecosystem service delivery and conserve species, habitats, and landscapes. Carpenter et al. (2009) also state that future research should focus on the controls on ecosystem services themselves, addressing the effects of multiple drivers, structural factors including biodiversity, and human feedbacks. Developing more effective ways to integrate biodiversity and conservation concerns with sustainability of ecosystem services remains an important goal.

Ecosystem Services: Synthesis

Ecosystem services and landscape sustainability offer rich opportunities for landscape ecology research and applications. Are relevant principles yet emerging from landscape ecology? Lindenmayer and Cunningham (2013) suggest six principles to be considered for managing forests as ecologically sustainable systems, and these seem like a broadly applicable set that bear consideration. These principles are: (1) Landscape management problems are often derived from human-use drivers that overcommit natural resources and undermine the ecosystem services that support and replenish these resources. In other words, human demand is typically driving the problems. (2) Not all parts of a landscape are equal in their contribution to species persistence and ecological processes. There are spatial disproportionalities, hot spots and cold spots, and spatially variable trade-offs. (3) Managing connectivity is critical, but it is essential to determine what kind of connectivity is desirable, and for what species and processes. Connectivity per se is neither good nor bad; rather, its value depends on what is being connected. (4) Land-use practices can produce spatial and temporal cumulative effects with negative impacts on biodiversity and ecosystem processes. Thus, actions and interventions ought not to be assessed in isolation. (5) Land-use decisions on the land sparing–land sharing spectrum are highly scale and context dependent. As seen throughout this book, scale matters! (6) Our understanding of landscape-scale processes is shaped by our conceptual model of the landscape.

The landscape ecology of ecosystem services is a rich area of research, but caveats are appropriate, as well. Although the wide availability of land-cover data make it tempting to use land-cover proxies to map ecosystem services, such proxies have proven to be poor fits to primary data on biodiversity, carbon storage, and recreation (Eigenbrod et al. 2010), indicating the better biophysical indicators and process-based models are needed. Correlations between ecosystem services also change depending on whether primary or proxy data are used (Eigenbrod et al. 2010), which means that assessments of trade-offs and synergies will be sensitive to the selection of indicators. As with modeling and landscape analysis, uncertainty must be assessed when ecosystem services are estimated; Hou and Müller (2013) provide a useful summary of sources of uncertainty and approaches for estimating uncertainty.

Ecosystem services and landscape sustainability will continue to be exciting areas of policy-relevant research, offering tremendous opportunities for contributions from landscape ecologists. Where is this field headed? In prioritizing questions designed to move from theory to practice, Carpenter et al. (2009) included several with clear landscape context: What combinations of ecosystem services can flow sustainably from particular landscapes? How do changing land use, nutrient mobilization, species composition, and climate affect flows of ecosystem services? For a given landscape, what drivers can be managed, and how? Five research questions at the frontier of landscape sustainability science were highlighted by Turner et al. (2013) and are summarized below. These questions also integrate much of the material that has been covered in this book (reproduced with some modification from Turner et al. 2013):

(1) *What types and levels of spatial heterogeneity contribute to sustained production of ecosystem services and what types and levels do not?* Landscapes are dynamic, all landscapes are unique (Phillips 2007), and there is no optimal landscape mosaic that can increase all ecosystem services. Rather, the composition and configuration of a landscape may enhance or sustain one bundle of ecosystem services and leave others vulnerable to degradation. Understanding the relationships between landscape heterogeneity and the provisioning of ecosystem services within different kinds of landscapes is the foundation from which trade-offs, synergies, trajectories, and management alternatives can be considered. How are the types and amounts of spatial heterogeneity that promote sustainability to be defined? If maintaining a set of ecosystem services within set bounds is desired, what kinds of alternative patterns promote those levels of production? Spatial heterogeneity may allow adaptation to future environmental change and help to sustain some ecosystem services, but humans often rescale or reshape natural heterogeneity. How can

land managers determine the types of spatial heterogeneity that will enhance or impede production of different ecosystem services? The science of landscape ecology can help to sort out the consequences of different kinds of spatial heterogeneity, including those that mimic natural patterns, for ecosystem services.

(2) *Where on the landscape do suites of ecosystem services respond similarly or in opposite directions to anticipated changes, and what are the mechanisms behind such synergies and trade-offs?* Understanding the kind, amount, distribution, and patterning of multiple ecosystem services on the landscape is critical for evaluating synergies and trade-offs among ecosystem services. By quantifying and mapping different ecosystem services, "hot spots" of ecosystem services can be readily identified, along with areas where conflicts over provision of differing ecosystem services are likely to occur (Steffen 2009; Qiu and Turner 2013) or thresholds may be exceeded (Raudsepp-Hearne et al. 2010). In forested landscapes, hot spots of ecosystem services often coincide with higher species and functional diversity (Lavorel et al. 2011). Managing spatially explicit relationships among different ecosystem services can strengthen landscape resilience, enhance the provision of multiple services, and help avoid catastrophic shifts (i.e., abrupt losses or declines) in ecosystem service production (Bennett et al. 2009).

(3) *What are the implications for resilience and vulnerability of ecosystem services of anticipated trajectories of landscape change?* Anticipating landscape changes and how the benefits people derive from a region will be affected by such changes are difficult, but methods from landscape ecology can contribute to addressing this challenge. Landscape ecology offers well-developed methods for projecting alternative landscape patterns probabilistically and for evaluating the consequences of landscape composition and configuration for different responses (e.g., Perry and Enright 2006; Gude et al. 2007; Berland et al. 2011). These methods can be incorporated into studies that explore future scenarios for ecosystem services. Trajectories of change that lead to sustained or enhanced ecosystem services can then be distinguished from those that cause ecosystem services to decline.

(4) *To what degree can landscape pattern be purposefully managed to enhance the resilience of ecosystem services in the face of changing drivers?* This, perhaps, is one of the largest challenges for landscape sustainability—maintaining the capacity for the landscape to produce ecosystem services in the face of change. Just how much leverage can be gained from "smart" management of land-use or strategic interventions to alter landscape patterns? Understanding the mechanisms behind synergies and trade-offs among ecosystem services can help identify ecological leverage points where small management investments can yield substantial benefits (Bennett et al. 2009; Qiu and Turner 2013). But how much can be gained by manipulating landscape patterns, and under what conditions will the magnitude of changes in some drivers overwhelm the importance of landscape heterogeneity? Landscape managers can intervene in some drivers to sustain ecosystems services (e.g., land-use planning can minimize effects on biodiversity) but have little influence

on others (e.g., society may have to simply adapt to climate-induced changes in fire regimes). Managers must know when landscape management can and cannot mitigate undesirable changes.

(5) *How well will understanding of past landscape dynamics and ecosystem services inform the future?* For many regions, predicted future conditions differ vastly from past and current conditions. Some studies suggest that "no-analog" communities will develop in the future (Williams and Jackson 2007), and others indicate that disturbance frequency may exceed that documented throughout the Holocene (Westerling et al. 2011). Concepts such as the historical range of variability (HRV; Keane et al. 2009) provide a baseline characterization of past landscape structure, function, and dynamics, from which we will be able to detect when a given landscape has moved beyond the historical condition as a result of changing climate, disturbance, and land-use drivers. However, the historical condition may not be a suitable restoration target if these drivers move landscapes well outside their HRV (Thompson et al. 2009). Will the relationship between future landscape patterns and production of ecosystem services change fundamentally from that of the past? Can approaches from landscape ecology help scientists and managers anticipate or avoid undesirable surprises?

Guaranteeing the continued provision of ecosystem services in the face of environmental change—maintaining functional landscapes that ensure human well-being—is the most pressing challenge in sustainability science, and contemporary landscape ecology has much to offer. As Daily et al. (2009) state, we must develop an ecosystem services framework that is credible, replicable, scalable, and sustainable. The role of landscape heterogeneity in buffering environmental variation, enhancing ecosystem resilience, and forestalling transitions past threshold to alternative states may be key to landscape sustainability, but it has been relatively little explored (Wiens 2013). How successful we are at steering our landscapes onto sustainable pathways may well determine our collective future.

SUMMARY

Landscape ecology has become essential for a variety of problems in applied ecology. Natural resource professionals have shifted their emphasis from management of separate resources to management focused on the integrity of entire ecosystems and landscapes. This shift in management has revealed the importance of spatial interdependencies among landscape components and created a demand for the inclusion of landscape ecology into resource management decisions at a broad range of spatial and temporal scales.

The expansion of resource management to regional scales prompted the development of landscape indicators, which can simplify analysis while quantifying the ecological effects of changes in the amount and arrangement of land cover. A reasonable array of landscape indicators has been proposed and their utility has been demonstrated in a number of settings. Useful indicators must meet several criteria, and landscape indicators should be part of any monitoring program to detect and quantify regional ecological change.

Among the applied challenges facing contemporary landscape ecologists, understanding and anticipating the effects climate and land-use change on landscape structure, function and sustainability are perhaps the most important. The potential impact of climate change on species and habitat distributions, agricultural production, water resources, and disturbance regimes is profound. The maintenance and/or restoration of pathways that facilitate species movements are important to maintain viable populations via dispersal and establishment processes as climate alters the locations of suitable habitat. Land-use activities change landscape structure by altering the relative abundances of natural habitats and introducing new land-cover types. A predictable land-use transition is observed as natural ecosystems are transformed by human activities. The rate of land-cover change has accelerated worldwide, particularly in regions with rapid population growth. Land-use change is affecting urban and rural landscapes alike, and research on urban landscapes has increased in recent years. Low-density rural housing development has increased substantially in the US, driven in part by people's desire for environmental amenities. Landscape ecologists were among the first scientists to recognize the need for more holistic approaches to understand and conserve habitats across the rural-to-urban development gradient, and they continue to advance this field.

Landscapes are not affected by single factors acting individually and independently. Rather, landscapes respond to multiple factors acting across a wide range of scales and which may interact. A key challenge—and opportunity—for landscape ecologists is to elucidate the relative influence of different drivers and the degree to which LULC patterns can be purposefully designed to mitigate environmental problems. Determining what patterns of land use will be in the future or should be to optimize oft-competing goals is not easy. In response to the need to anticipate future conditions in the face of tremendous uncertainty, scenarios have proven very useful for exploring implications of changes in land use and other drivers of landscape pattern. Different approaches to scenario development serve different purposes, but they have been used effectively at national and regional scales to explore plausible futures. From a practical standpoint, there is much to be learned regarding how much the decisions about how much and where to arrange different LULC elements affect the ability to reach some desirable goal, and the degree to which landscape patterns may mitigate or amplify the effects of other drivers.

A key reason for considering future climate and land-use change in landscape ecology, and for using scenarios to explore plausible future conditions, is the shared goal of sustaining the structure and function of landscapes for decades to come. One way to approach this goal is by considering ecosystem services or the benefits that people obtain from ecosystems. Sustainability refers to use of the environment and resources to meet current needs without compromising the ability of a system to provide for future generations. We emphasize the capacity of landscapes to deliver desired ecosystem services in the face of human land use and a fluctuating environment, now and in the future, which we call landscape sustainability. Assessing, projecting, and managing the flows of ecosystem services across spatially heterogeneous landscapes are important topics in sustainability science, but the spatial ecology of ecosystem services is not well understood. Studies to date now suggest that promoting regional land-use diversity is the major opportunity for maintaining ecosystem services and biodiversity outside of conservation areas. Spatial analyses have shown that landscape connectivity is another key attribute that must be maintained because lateral movements of organisms and matter are essential components of many ecosystem services. Anticipating future production and delivery of multiple ecosystem services as various drivers change is a critical component of landscape sustainability. Interdisciplinary research teams are beginning to address this by modeling alternative future landscape conditions and their potential consequences for multiple ecosystem services. Managing the landscape to provide multiple services is challenging because the optimal arrangement for one ecosystem service may be very different from the optimal arrangement for another.

Parting Comments

Are there lessons that can be extracted thus far from applications of landscape ecology? We think so. First, determining what is "optimal" for any given landscape is not straightforward. "Optimal" is a value judgment, and the development of a consensus opinion is often an arduous process. It is difficult to balance the multiple criteria by which a landscape may be considered sustainable—economic output, human well-being, persistence of biodiversity, maintenance of water quality, and adequate land for human development. Even when "naturalness" is identified as a goal for landscape condition, implementing such an objective is not straightforward. The landscape ecologist can provide a rigorous analysis of alternative landscapes, including the potential implications for various ecological processes. However, the science still stumbles when an optimal target condition must be unambiguously identified—in part, because such a decision requires more than science. This is where scenario approaches play an especially important role.

Second, applied landscape ecology is most effective as a team approach; indeed, none of the work highlighted in this chapter has resulted from single-investigator science! This means that landscape ecologists must be attentive to the requirements of building effective teams; Likens (1998) nicely summarized many of the factors that so strongly influence the effectiveness and productivity of collaborative (and often interdisciplinary) research (Table 9.4). We strongly recommend that collaborative research be encouraged—and rewarded—at all levels, and that graduate training include opportunities for team research and interdisciplinary study. Furthermore,

Table 9.4.
Characteristics needed for building an effective team to conduct effective research in ecosystem science (Likens 1998).

1. Brightness
2. Trusting/trustworthy
3. Abundant common (or good) sense
4. Creativity and willingness to share
5. Appropriately trained
6. Collective ability to make up deficiencies
    - Shared experiences
7. Willing to give team time.
8. Personality
    - Ability and willingness to listen
    - Enjoy working with other people
    - Curiosity and interested
    - Openness of mind
9. Keeping eyes open (serendipity reigns)
10. Liking each other

[Luck helps!]

Applications of landscape ecology also usually require a team approach, and these factors should be helpful when building an effective team.

practical applications of landscape ecology involve communication between scientists and decision-makers. It is increasingly important that scientists and practitioners develop communication skills geared toward policy makers and the public.

Third, there is an urgent need for landscape ecologists to be trained in advanced analytical methods, including modeling, spatial statistics, and remote sensing. Modeling offers a means for exploring the causes and consequences of alternative spatial patterns. But the integration of models, and their evaluation, is a technologically challenging process. Greater exposure to the development, parameterization, and interpretation of models should be required in the training of landscape ecologists. Landscape ecologists must have more than a passing familiarity with model development and interpretation, as well as techniques for quantitative spatial analysis.

Fourth, there will never be "enough" data upon which to base management recommendations. GIS databases are now very common in land and resource management, and so some of the tedious work required to build databases for landscape analysis and applications has been reduced. However, there are still never enough spatially explicit data—for species occurrence, demography, or dispersal; water quality; productivity or nutrient dynamics; and the like. As is true for other areas of ecology, landscape ecologists should recognize that decisions must and will be made in the face of uncertainty, and that "the data" represent only one of the inputs to the decision-making process. The best current science and data must be brought to bear upon applied questions, with full recognition that our understanding may well change in the future.

Finally, applications of landscape ecology require integration and synthesis. Throughout this book, and as students are typically taught, concepts are separated into seemingly discrete units—e.g., species responses to landscape patterns, disturbance dynamics, or spatial patterns of nutrient cycling. In landscape ecology applications, however, these separate concepts must be considered synthetically. Therefore, thinking across traditional boundaries must be encouraged. We are optimistic that applications of landscape ecology will continue to develop, and that applied problems will continue to stimulate progress in our basic understanding of the relationship between pattern and process at multiple scales.

Guaranteeing the continued provision of ecosystem services in the face of environmental change—maintaining functional landscapes that ensure human well-being—is the most pressing challenge in sustainability science, and contemporary landscape ecology has much to offer. The role of landscape heterogeneity in buffering environmental variation, enhancing ecosystem resilience, and forestalling transitions past threshold to alternative states may be key to landscape sustainability.

DISCUSSION QUESTIONS

1. Define, compare, and contrast "basic" and "applied" research in landscape ecology. Do you think the distinction is useful? Why or why not?
2. You have been named the director of the newly created Agency for Monitoring Landscape Change (AMLC). Your charge is to develop a set of landscape indicators that can be used to detect change through time and differences among landscapes in a region (*select a regional landscape of your choice*). Develop a set of at least five landscape indicators that will constitute your initial monitoring plan for the AMLC. For each indicator, describe: (a) what attributes of the pattern and process of the landscape the index measures, and (b) the advantage and limitations affecting its use. Explain why the set that you have selected will best meet the needs of the AMLC, i.e., justify your choices based on what the set will accomplish in to.

3. For the landscape you selected above, describe how climate and land use may change in the future. State expectations for how your set of landscape indicators will change in the future. Explain the significance of those changes in terms understandable to regional land managers and citizens.
4. Climate change may have immediate as well as long-term effects on ecosystem services delivered by diverse ecosystems. List 2–3 key services provided by temperate forests, streams, and lakes. Speculate on those aspects of climate change (e.g., changes in temperature and precipitation, frequency of storm events, etc.) which may have immediate (discernable) effects or cause long-term changes in ecosystem attributes.

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CHAPTER

10

CONCLUSIONS AND FUTURE DIRECTIONS

As we reflect on the advances, topics, and wide range of studies included in this second edition of *Landscape Ecology in Theory and Practice*, it is gratifying to see how landscape ecology has matured. Motivated by broad-scale environmental challenges and facilitated by rapid developments in computing power and technology, landscape ecology has emerged as a synthetic discipline that has generated new concepts, theory, and methods that reveal the importance of spatial pattern in ecological systems. Landscape ecology is now a well-recognized subdiscipline in ecology as well as an interdisciplinary area of research and application that embraces social–ecological systems and extends well beyond ecology. The many landscape studies published in a diverse array of journals also speak to the importance and impact of landscape ecology. In this book, we have emphasized current ecological understanding of the causes of spatial pattern, reciprocal interactions between spatial patterns and ecological processes, and how these patterns and processes change through time. In this final chapter, we summarize some general lessons from landscape ecology and suggest several promising directions for future research.

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WHAT HAS BEEN LEARNED FROM LANDSCAPE ECOLOGY?

It is difficult to distill from an entire book, which is already a distillation of a vast primary literature, summary statements about what has been learned from landscape ecology. Recognizing the potential pitfall of superficiality, we nonetheless suggest a few general insights that emerged directly from the growth and development of the discipline.

First and foremost, landscape ecology has clearly demonstrated that spatial heterogeneity is an important influence on a wide range of ecological patterns and processes. It is now expected that ecologists meaningfully consider spatial pattern as a potential factor influencing ecological responses, regardless of whether they study individual organisms, populations, communities, or entire ecosystems. Consideration is expected at all phases of a study: research initiation, when questions and hypotheses are formulated; experimental design, when sampling protocols and scales are established; and analysis, when spatial autocorrelation and generalizability must be addressed. Second, landscape ecology has also demonstrated the unambiguous influence of scale on analyses and interpretations and provided quantitative methods for addressing scale issues. Third, landscape ecology has provided tremendous insight into ecological dynamics over areas of broad spatial extent, and much of that understanding laid the groundwork for continental-scale environmental science (Peters et al. 2008, 2014) and current frameworks such as *macrosystems ecology* (Heffernan et al. 2014).

In an early essay (Turner et al. 1995a), we summarized insights relating to ecological dynamics at broad scales with a particular emphasis on biodiversity. In the first edition of this book, we extended that list to consider contributions of landscape ecology more broadly, and here, we augment that list once again.

- All landscape have a history. The complex patterns observed on today's landscape result from many causes, including variability in the abiotic template, biotic interactions, natural disturbances, and both past and present patterns of human settlement and land use. However, every landscape is unique, and spatial and temporal contingencies are of remarkable importance in shaping the current state of any given landscape. Multicausality and interacting drivers are the rule, not the exception.
- There is no single "right" scale for all landscape ecological studies. The appropriate scale depends on the question being asked and the processes being studied; pattern–process interactions involving organisms must be studied at scales appropriate for the organism or process of interest. Therefore, scale effects must be considered carefully in all studies. Mismatches in scale often result in misleading, contradictory, or wrong answers.

- Many metrics are available for quantifying landscape patterns, but many are correlated with one another. One metric is insufficient to characterize a landscape, but determining how many and which ones to use must be based on the questions or objectives of a study and well justified by the analyst.
- Landscape pattern includes both composition and configuration. When using any metric of landscape configuration, it is critically important to account first for effects of landscape composition because the amount of different cover types in a landscape constrains the possible types and arrangements of spatial pattern.
- Landscape structure does not equate to landscape function. Although it is tempting to make that assumption, it is necessary to demonstrate and test pattern–process relationships.
- Disturbances create and respond to landscape heterogeneity, and landscapes are strongly shaped by their disturbance regimes. Shifting disturbance regimes and interactions among disturbances may lead to abrupt changes in landscape patterns and processes. Spatial effects of disturbance on succession become stronger when residuals are few or sparse and disturbance patches are large.
- Characteristics of the surrounding landscape can strongly influence local populations. Thus, it is important to consider local conditions as well as landscape context when explaining the presence and abundance of organisms in a landscape.
- Populations and a wide range of interactions among species produce important feedbacks to ecosystem processes and landscape patterns.
- Elements of the landscape may serve as sources or sinks for nutrients that move between ecosystems, including transfers—in both directions—between terrestrial and aquatic systems.
- Human influences (e.g., land-use change) are dominant factors controlling ecological dynamics at broad scales. Land use may amplify or dampen the effects of other drivers, and it is increasingly important to understand such interactions.
- Maintaining ecologically functional landscapes is critical for sustaining human well-being. Landscape ecology plays an important role in managing for the capacity of landscapes to deliver desired ecosystem services in the face of human land use and a fluctuating environment, now and in the future.

Another perspective on lessons learned from landscape ecology was offered by Jingle Wu, current editor-in-chief of *Landscape Ecology,* who synthesized the field to mark the 30-year anniversary of the Allerton Park Workshop (Wu 2013). The workshop was held in April 1983 (Risser et al. 1984) and established, in part, the foundation for modern landscape ecology. Wu's analysis led to his top-10 list of topics for which advances in landscape ecology are especially notable: (1) pattern–process–scale relationships, including hypothesis development and testing;

(2) landscape connectivity and fragmentation; (3) scale and scaling; (4) spatial analysis and landscape modeling; (5) land-use and land-cover change; (6) landscape history and legacy effects; (7) landscape and climate change interactions; (8) ecosystem services in changing landscape; (9) landscape sustainability; (10) accuracy assessment and uncertainty analysis. Indeed, advances are obvious in all of these areas. As Wu (2013) asserted, progress in landscape ecology has been swift, and the field remains dynamic and vibrant. We wholeheartedly agree!

FUTURE DIRECTIONS

With its emphasis on spatial pattern and scale, a landscape focus in ecology is here to stay. Contemporary landscape ecology continues to build on many themes that are at the core of the discipline while also embracing new directions and challenges. What frontiers are likely to drive research and lead to new insights during the coming decade? In the first edition of this book, we identified six pressing research directions. Here, we revisit those topics and comment on progress since that time. We then offer thoughts on current research challenges and priorities and comment on additional skills we think are important for meeting the needs of future landscape ecologists.

Future Directions Revisited from the First Edition

Spatial heterogeneity and ecosystem processes. When we wrote the first edition, understanding of ecosystem processes in the landscape—how rates vary over space and at different spatial scales, and what controls this variation—was in its infancy (Carpenter and Turner 1998). We suggested that the integration of landscape and ecosystem ecology should be a high priority, and as is evident in Chap. 8, progress has been substantial. This remains an exciting area of research, especially as the implications of multiple environmental drivers (e.g., climate change, land-use change, and shifting disturbance regimes) for ecosystem processes receive continued attention.

*Relating landscape metrics to ecological processe*s. Following the very rapid development of landscape pattern metrics through the 1990s, we had identified three major areas in which further understanding was sorely needed: (1) the statistical properties and behavior of metrics needed to be better understood, (2) the relative sensitivity of different metrics to detecting changes in the landscape was not known, and (3) the empirical relationships between landscape patterns and ecological processes of interest needed to be better documented and the underlying mechanisms understood. Progress has been made in each of these three research areas, which has helped landscape ecologists determine what is worth measuring and why, and understand when a change in a metric is statistically and ecologically significant. The set of metrics has largely stabilized, and most practitioners are knowledgeable about their appropriate use. However, spatial statistics have advanced tremendously through the 2000s, and integrating different approaches to quantifying spatial heterogeneity—especially the degree to which they provide complementary and/or unique insights about landscape pattern—remains a priority.

Thresholds, nonlinearities, and rules for scaling. Critical thresholds in landscape pattern have important implications for understanding relationships between spatial patterns and processes, and we advocated for more work on this topic. Thresholds in ecology are now widely recognized (Groffman et al. 2006b), and consequences of suddenly connecting or disconnecting landscape elements have been explored in a range of systems. Effects of scale are also well recognized, although the need for improved quantitative understanding remains critical. Nonlinear dynamics and scaling are topics that will continue to motivate a considerable volume of basic and applied research in landscape ecology.

Feedbacks between organisms and ecosystems in space. Identifying spatial interactions and feedbacks between organisms and ecosystem processes was identified as an important goal for landscape ecology. Empirical understanding of such interactions has grown tremendously, particularly because of major advances and increased affordability of technologies for monitoring movement in real time. In addition, the library of empirical studies that quantify how organisms affect patterns of ecosystem process rates has also grown. Extending these approaches to consider how species–ecosystem interactions respond to environmental change will be important in the future.

Causes and consequences of land-use change. We noted previously that the size of the human population on earth had reached six billion during the fall of 1999, and that humans were transforming much of the surface of the earth and co-opting much of the world's resources (Vitousek et al. 1997a). The size of the human population reached seven billion in 2011 and continues to increase, though the rate of increase is declining. Indeed, the age in which we live has been called the Anthropocene (Ellis et al. 2010b). Human land use is primary drivers of landscape change worldwide, and understanding causes and consequences of land-use change was and still is a high priority topic in landscape ecology. Land-use patterns and their changes are spatial phenomena, and landscape ecologists must contribute toward understanding and predicting these patterns and their ecological consequences. This area should continue to receive attention from landscape ecologists and should include understanding land-use legacies and how choices made today will impact landscapes long into the future.

Sampling. Landscape ecology is not constrained to asking questions over large areas, but many landscape ecological studies do so. The problems inherent in sampling across large regions in a way that permits inference of the effects of spatial heterogeneity remain challenging. We called out the need to develop improved ways of sampling over large areas, using appropriate (and possibly new) statistical methods for data analysis, and creative combinations of methods, including field sampling, experimentation, remote sensing, and modeling. Progress has been substantial, but the need remains great, particularly as ecological studies emphasize regional to continental extents, and new broad-scale monitoring programs are anticipated.

Collectively, these six research directions contribute toward furthering knowledge of what Wiens (1999) summarized as the four central themes of landscape ecology: spatial variation, scaling, boundaries, and flows. Progress in each area has been substantial, and landscape ecology research has complemented understanding obtained from research at other levels in ecology. A spatially explicit view of ecological systems has enhanced integration across traditional boundaries in ecology.

Looking Ahead

After looking back, what directions now seem most promising? While it is gratifying to reflect on how much progress has been made in landscape ecology over the past 15 years, it is also exciting to think about new avenues of research that have emerged and the role that landscape ecology can continue to play in the future. There is no shortage of questions to be addressed, and we hope that this book provides a foundation and motivation for the development of new studies in landscape ecology. We have organized questions into several general themes (Table 10.1). While landscape ecology has clearly matured, many exciting challenges and opportunities lie ahead.

Interactions among multiple drivers. Landscape patterns result from multivariate causes operating over many scales, and they can still be difficult to predict. Much progress has been made in understanding the consequences of single drivers, but elucidating interacting drivers remains a challenge. Drivers interacting at different scales of space and time can produce surprising and sudden changes in landscapes, but a general understanding of such dynamics is lacking.

Climate change. Climate change is a reality, and it will influence landscapes in myriad ways in the decades ahead. Understanding these changes and how to mitigate undesirable consequences or adapt our landscapes to enhance resilience is of paramount importance. Landscape patterns will influence ecological responses to climate change, and landscape patterns will themselves change.

Changing disturbance regimes. Disturbance has been a prominent theme in landscape ecology for 25 years, and much has been learned regarding the pattern–process dynamics of disturbances. However, disturbance regimes are changing, and understanding the ecological consequences of such regime shifts is more important than ever.

TABLE 10.1.
AN ILLUSTRATIVE SET OF RESEARCH QUESTIONS THAT REPRESENT SOME OF THE CURRENT FRONTIERS IN LANDSCAPE ECOLOGY.

Theme	Questions
Interactions among multiple drivers	What is the relative importance of different factors in producing landscape patterns? How well can we explain the patterns we observe?
	How do relationships among drivers vary with scale?
	How do different causes of pattern (abiotic template, climate, biotic interactions, disturbance, human land use, sociocultural factors) interact?
	Under what conditions are cross-scale interactions among drivers of particular importance? For example, when do interactions lead to tipping points?
Climate change	How, when, where, and why will landscapes change qualitatively as climate warms?
	How does landscape composition and configuration interact with climate change and influence future distributions of species? What conditions will enhance spread of nonnative invasive species? When are no-analog communities likely?
	To what degree can landscape management be used to mitigate undesirable consequences of climate change?
	What are the critical feedbacks and time lags in climate–landscape interactions?
Changing disturbance regimes	How will changing disturbance regimes affect landscape patterns and processes? Where are surprises likely?
	How do altered landscapes influence disturbance regimes?
	How will postdisturbance trajectories in the future differ from those of the past?
	How should management anticipate changes in disturbance regimes? Where will changes be of greatest magnitude? How can landscapes be designed or managed to enhance resilience to disturbance?
Behavioral landscape ecology	How much do individuals of the same species vary in their behavioral responses to landscape heterogeneity?
	What are the effects of natal vegetation type, edge types, and matrix conditions on intraspecific differences in behavioral decisions and movement ability?
	How do cues from conspecifics influence dispersal and habitat selection?

(continued)

Table 10.1. *(continued)*

Theme	Questions
Species interactions and biotic communities	How does landscape heterogeneity influence interactions between species? What components of species interactions (e.g., detections, encounter, chase, escape) are affected by pattern?
	Do some landscapes disrupt species interactions? Do other landscapes facilitate species interactions? To what degree can landscapes be managed to influence species interactions?
	How does spatial heterogeneity influence entire biotic communities? How are changes in species assemblages affected by landscape heterogeneity?
	What features of landscapes promote homogenization vs. diversification of community structure?
Landscape genetics and evolution	What is the role of landscape features in driving genetic variation, and is the landscape influence overrated?
	How does the past shape contemporary genetic variation?
	How does spatial heterogeneity contribute to microevolution, and what are the implications of rapid changes in landscape pattern for adaptive genetic variation?
	Which statistical methods should be used for explaining landscape effects on genetic variation? What are the pros and cons of different approaches?
Ecosystem processes	How do rates of ecosystem processes vary over space and at different spatial scales, and what controls this variation?
	When must spatial contingencies be considered?
	How can landscape/regional dynamics be captured in global models?
	How can/should models be scaled up or scaled down?
Land-use change	What are the future legacies of contemporary land-use patterns and decisions for patterns, processes, and options?
	What types of land-use patterns enhance landscape resilience and/or buffer landscapes from undesirable consequences of other environmental drivers?
	How can landscape ecology contribute to a good Anthropocene?

(continued)

Table 10.1. *(continued)*

Theme	Questions
Spatial aspects of social–ecological systems	What spatial patterns enhance resilience in social–ecological systems?
	How do the spatial scales of institutional policies and individual decision making align with landscape patterns and processes, and what are the consequences of mismatches in scale?
	What events or conditions elicit societal (or individual) responses? Do people respond in time to prevent undesirable or irreversible ecological change?
Ecosystem services and landscape sustainability	What types and levels of spatial heterogeneity contribute to sustained production of ecosystem services and what types and levels do not?
	Where on the landscape do suites of ecosystem services respond similarly or in opposite directions to anticipated changes, and what are the mechanisms behind such synergies and trade-offs?
	What are the implications for resilience and vulnerability of ecosystem services of anticipated trajectories of landscape change?
	To what degree can landscape pattern be purposefully managed to enhance the resilience of ecosystem services in the face of changing drivers?
	How well will understanding of past landscape dynamics and ecosystem services inform the future?

Adapted from Knowlton and Graham (2010), Turner et al. (2013), Bolliger et al. (2014) and Turner (2015).

Behavioral landscape ecology. Populations have been well studied in landscape ecology, but the richness of variation in behavior among individuals (among whom responses to spatial patterns can differ a lot) and how these spatial interactions translate into dynamics at higher levels of organization is only beginning to be explored and understood.

Species interactions and biotic communities. Much has been learned about the dynamics of single species in heterogeneous landscapes. However, species interactions (e.g., competition, herbivory, predation, mutualism) in heterogeneous landscapes, and how spatial patterns influence entire biotic communities remains a frontier. Furthermore, few studies have explored reciprocal, iterative interactions between organisms and landscape patterns over the long term.

Landscape genetics and evolution. Landscape genetics offers exciting new directions for examining within-species variation and bridging to evolution. This is especially important for understanding adaptive variation, as selective forces play out on heterogeneous landscapes. The preservation of genetic diversity of populations within fragmented landscapes is a new challenge for conservation of threatened and endangered species.

Ecosystem processes. Despite early representation of ecosystem ecology within landscape ecology, explaining and predicting heterogeneity in ecosystem processes across landscapes remains a challenge. In part, this is because of scaling challenges: many ecosystem processes are microbially mediated and operate at very fine scales, yet we may wish to predict the broad-scale patterns that result. At the other end of the spectrum, global-scale models do not incorporate the regional variation that is often at the core of landscape studies.

Land-use change. Humans will continue to alter landscapes. Landscape ecology can provide crucial information about the consequences of those alterations and how land can be managed for enhanced sustainability. We have many opportunities to understand the degree to which land use can be guided in ways that buffer landscapes from other environmental drivers.

Spatial aspects of social–ecological systems. Humans have always been recognized in landscape ecology as important components of the system. The emergence of widespread interest in social–ecological systems should provide an opportunity for landscape ecology to contribute in meaningful ways.

Ecosystem services and landscape sustainability. Ecosystem services, the benefits that people obtain from ecosystems, are often affected by spatial heterogeneity. Again, landscape ecology has an opportunity to make important contributions to ongoing research in sustainability science.

Training the Next Generation of Landscape Ecologists

When training the next generation of landscape ecologists, what should be emphasized in addition to high-quality science and application? Learning to ask and answer good questions—those that are of general interest and importance, and answerable—and disseminate that new knowledge is arguably the most important goal of graduate training. However, that alone is not sufficient to be effective in basic and applied landscape ecology. Here, we highlight areas that we consider especially important when looking toward the future.

Build effective collaborations. Practically speaking, much effort in landscape ecology involves collaborative teams. We encourage landscape ecologists to think carefully and be deliberate in organizing collaborative teams so that they reach their potential. Successful collaborations produce outcomes that surpass the accomplishments of any one individual, but this does not happen by accident. High-performing teams share a set of characteristics that include positive interdependence of team members, effective communication, and accountability as individuals and groups (Cheruvelil et al. 2014). We have both had the experience of being members of highly effective collaborations, and in a good team, the whole is definitely greater than the sum of the parts. New communication technologies have afforded many new channels for interactions among team members, which is very helpful. However, there remains no substitute for the quality of interaction gained from face-to-face meetings. As we train future landscape ecologists, we must set good examples, provide opportunities for junior scientists to develop collaborative tools, and nurture the skills needed for effective participation in local to global research teams.

Encourage interdisciplinary thinking. Humans have always had a place at the landscape ecology table, but anticipating and managing future landscapes requires embracing the linkage between social and ecological systems and the properties that make such systems resilient or vulnerable in the face of change (Chapin et al. 2009b). The goal of establishing functional landscapes that are sustainable of the long term motivates much work in landscape ecology. Most ecologists are not trained in the social sciences, and most social scientists are not trained in the natural and physical sciences. The academic cultures differ substantially, but the challenges faced by society require us to work together. Recognizing that our students need disciplinary depth in their training, we must nonetheless encourage a much greater appreciation for the linkages among disciplines.

Understand models and modeling. Quantitative models are widely used in landscape ecology (and in all of science), yet a general decline in the training of ecology students in modeling has been noted for some time (Canham et al. 2003). This is problematic. Models serve so many important purposes, from formalizing understanding to produce testable hypotheses, to exploring a wider range of conditions than can be studied empirically. We provided an overview of landscape modeling in Chap. 3, but much deeper understanding of how to build, use, and interpret models is needed in landscape ecology. We encourage faculty to train students in modeling, and students to seek opportunities to learn these approaches.

Welcome big data, but use responsibly. The amount and variety of data that are now readily available is opening up whole new questions and ways to answer those questions. Just think about how open access to the entire archive of Landsat imagery, or the advent of Google Earth™, has influenced landscape studies. Many other data sources are now readily available, and this trend will likely continue. While traditional scientific methods will not be supplanted, new approaches to using *big data* will become part of our toolbox in landscape ecology. This is likely to involve working with new kinds of infrastructure and networks (Peters et al. 2014) in which landscape ecologists should participate. For established scientists, this will mean training our students differently from how were trained, but ways that prepare them to be leaders in emerging frontiers. However, big data is not a panacea for broad-scale ecology. The old computer maxim, “garbage in, garbage out” also applies here, and it is incumbent upon the user to fully understand the data sources and their quality, limitations, and appropriate use.

Don't hide behind the computer. Although quantitative methods and simulation modeling are widely used in landscape ecology, landscape ecologists must be intimately familiar with the systems they study and manage. Thus, make it a priority to spend time "in the field," regardless of the type of landscape you study. Stay well grounded in the real world! Exploring and collecting data in your study landscape often yields new questions; it also provides a reality check on computer-based analyses. Further, many landscape studies involve interacting with people. Listen to stakeholders, land owners, and land managers, and discuss your science with them. This will also yield new questions and valuable insights, while hopefully building understanding and appreciation among the public for science.

Communicate effectively. As is true for scientists in all fields, the next generation of landscape ecologists will be expected to communicate effectively to diverse audiences. It is not enough to communicate only within the discipline or to other specialists. Communication channels have proliferated as new media have emerged, and these multiple channels present opportunities and challenges. There are myriad ways to reach an audience, but doing so effectively and budgeting time take effort. Funding sources may diversify in the future, as well, and depend on more than just technical excellence. We must provide opportunities for students to hone their abilities to communicate effectively across multiple platforms to diverse public audiences (e.g., Baron 2010).

CONCLUSION

Landscapes are characterized by complexity, change, and scale dependencies. We remain very excited about the basic questions and applied challenges that face landscape ecologists (Table 10.1) and optimistic that significant progress will continue in the coming decades. Simple cause–effect relationships are unlikely in landscape systems, and this argues for a pluralism of approaches that embraces this complexity and recognizes the complementary roles of different research methods. Landscape ecologists must continue to learn about the causes of spatial heterogeneity in landscapes and how these patterns and their dynamics influence ecological processes. Instruction of the next generation of ecologists, resource managers, and landscape architects requires that landscape ecological principles be clearly defined and articulated. The potential contribution of landscape ecology (and landscape ecologists) to addressing the serious consequences of landscape change is enormous.

In conclusion, landscape ecology should lead the next generation of studies that take a comprehensive look at ecological dynamics in heterogeneous landscapes. The themes of landscape ecology—reciprocal interactions between pattern and process, heterogeneity, scaling, critical thresholds, and boundaries and flows—have enriched the discipline of ecology. Landscape ecology should continue to refine knowledge of when spatial heterogeneity is fundamentally important in ecology (and thus the inverse, when it can be ignored), rigorously test the generality of its conceptual frameworks, and focus on developing more mechanistic understanding of the reciprocal relationships between pattern and process. We trust that this text will be a stimulus for critical and productive discussion about how spatial pattern and ecological processes interact, and we hope it provides a foundation upon which new ideas, approaches, and applications of landscape ecology can continue to build.

DISCUSSION QUESTIONS

1. How has landscape ecology made *unique* contributions to ecology? In what ways is landscape ecology distinct vs. integral to ecology and/or other disciplines in which you work? Explain your rationale.
2. Some authors have suggested that landscape ecology catalyzed a paradigm shift within ecology. Do you agree? Define “paradigm shift,” then provide the rationale for your assessment.
3. You are the program officer in charge of $25 million of new funds targeted for cutting-edge research in landscape ecology. Write the one-page “Request for Proposals” (RFP) that identifies the areas for which you would want to see proposals submitted.
4. Table 10.1 includes many different research questions that are stated in very general terms but amenable to being answered specifically in particular landscape settings. Choose 1–3 questions and translate these into answerable questions in a landscape of your choice. Develop expectations or hypotheses for each.

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