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LANDSCAPE ECOLOGY IN NORTH AMERICA: PAST, PRESENT, AND FUTURE

MONICA G. TURNER[1]

Department of Zoology, Birge Hall, University of Wisconsin, Madison, Wisconsin 53706 USA

Abstract. Landscape ecology offers a spatially explicit perspective on the relationships between ecological patterns and processes that can be applied across a range of scales. Concepts derived from landscape ecology now permeate ecological research across most levels of ecological organization and many scales. Landscape ecology developed rapidly after ideas that originated in Europe were introduced to scientists in North America. Key research questions put forth in the early 1980s that catalyzed landscape-level research focused on the formative processes that produce spatial pattern; effects of spatial heterogeneity on the spread of disturbance and fluxes of organisms, material, and energy; and potential applications of landscape ecology in natural resource management. This article describes the development of landscape ecology in North America, discusses current questions and new insights that have emerged, and comments on future directions that are likely to produce new ecological insights. Ecology faces a broad array of challenging questions that require a plurality of approaches and creative insights. Landscape ecology should continue to push the limits of understanding of the reciprocal interactions between spatial patterns and ecological processes and seek opportunities to test the generality of its concepts across systems and scales.

Key words: landscape context; landscape ecology; scale; spatial heterogeneity; spatial pattern.

SPECIAL FEATURE

INTRODUCTION

Concepts derived from landscape ecology now permeate ecological research across most levels of organization and many scales; indeed, perhaps the widespread infusion of a landscape perspective in ecology indicates maturation of this field in North America. Landscape ecological research has contributed to substantial advances in understanding the causes and ecological consequences of spatial heterogeneity and how relationships between pattern and process vary with scale, and it has offered new perspectives on the function and management of both natural and human-dominated landscapes. Methods derived from landscape ecology receive widespread use, and the potential importance of spatial heterogeneity is now regularly acknowledged in ecology. Landscape ecology has become mainstream, in sharp contrast to the mid 1980s, when the ideas were new and broad-scale studies were not widely accepted. In this article, I consider the past, present, and future of landscape ecology in North America, focusing on major research themes, new insights that have emerged, and both current and future questions. I focus on the interface between ecological patterns and processes, and there is another body of research, not covered in this essay, that directly addresses landscape and urban planning (e.g., Nassauer 1997).

Landscape ecology has been defined variously (Risser et al. 1984, Urban et al. 1987, Turner 1989, Pickett and Cadenasso 1995, Turner et al. 2001), but shared among definitions is the explicit focus on the importance of spatial heterogeneity for ecological processes. Often, but not always, landscape ecology is also characterized by a focus on spatial extents larger than those traditionally studied in ecology. The scale-independent focus of landscape ecology on the causes and consequences of spatial heterogeneity is distinct from how landscape ecology is sometimes defined (e.g., Zonneveld 1990, Bastian 2001, Opdam et al. 2001). Although these two foci are not mutually exclusive, the different perspectives have created some confusion about what constitutes landscape ecology. Some researchers also consider the terrestrial terminology limiting (e.g., Reiners and Driese 2001), but landscape ecology is applied in aquatic and marine systems (e.g., Steele 1989, Bell et al. 1999, Teixido et al. 2002, Ward et al. 2002). The generality of the landscape perspective and its application across a wide range of systems and scales has certainly given it wider applicability within ecology, and studies focused on larger areas have contributed to new understanding of ecological dynamics.

THE PAST: DEVELOPMENT OF LANDSCAPE ECOLOGY IN NORTH AMERICA

"Landscape ecology" was coined by the German biogeographer, Carl Troll (1939), and the field subse-

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[1] E-mail: turnermg@wisc.edu

quently developed in central Europe in close association with land planning (Schreiber 1990). However, the term was largely absent from North American literature until the 1980s when several ecologists from North America attended European meetings focused on landscape ecology, some influential publications appeared, and a workshop concentrated thinking on the emerging discipline. A lexicon and framework for considering spatial patterns were introduced by Forman and Godron (1981) and developed further in their subsequent book (Forman and Godron 1986). A conceptual framework for considering the potential influences of patch configuration and boundary permeability on lateral fluxes was proposed by Wiens et al. (1985). Naveh and Lieberman (1984) promoted the concept of the landscape as a holistic, cybernetic system with a strong emphasis on integrating humans into understanding of landscape function. In his study of the natural fire regime in Yellowstone National Park, Romme (1982) extended concepts of species diversity to successional stages in the landscape, demonstrating nonequilibrium in a fire-dominated system. A 1982 workshop funded by the National Science Foundation brought North American ecologists together to explore the purview and potential of landscape ecology and to set out an initial research agenda (Risser et al. 1984). The first annual U.S. landscape ecology symposium was held in 1986 and focused on interactions between landscape heterogeneity and disturbance (Turner 1987); the U.S. chapter of the International Association for Landscape Ecology (US-IALE) was also formed at this meeting. The scope of landscape ecology as perceived by North American ecologists was further elaborated by Urban et al. (1987) and Turner (1989).

The new ideas about spatial heterogeneity found a receptive audience in North America, and landscape ecology began a period of rapid development. Publications indexed by the Institute for Scientific Information illustrate this trend; landscape ecology publications were scant throughout the 1980s (fewer than 10 per year through 1991) but have increased dramatically since the early 1990s (Fig. 1). Several factors contributed to this acceleration (Turner et al. 2001). First, important environmental challenges and land-management questions (e.g., global climate change, habitat fragmentation, nonpoint source pollution, cumulative effects, land-use change) were increasingly posed at broad scales, yet ecological understanding was based largely on mechanistic studies in small homogeneous areas over relatively short time periods. Other conceptual developments were also spurring new thinking in ecology. For example, the importance of natural disturbances (e.g., Romme 1982, Turner 1987) and patch dynamics (Pickett and White 1985) for ecosystem structure and function was increasingly acknowledged. Equilibrium theory was being critically questioned and considered more broadly (Wu and Loucks 1995, Perry 2002), and the temporal scale of ecological studies was

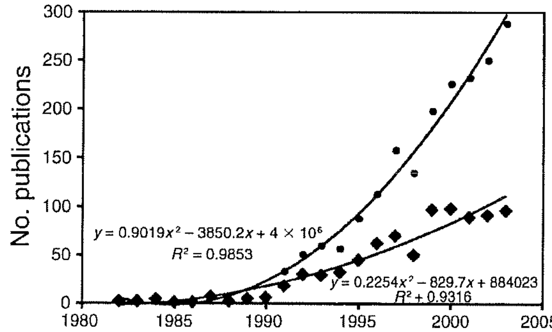

FIG. 1. Annual number of publications (1982–2003) from the ISI Web of Science database that included either "landscape ecology" (diamonds) or "landscape AND ecology" (circles) in their title, abstract, or key words. The search was conducted on 7 April 2004 using the science database only and including all document types. Trendlines were fit in Microsoft Excel.

being extended through new research programs, such as the National Science Foundation's Long-term Ecological Research (LTER) Program (Hobbie et al. 2003). Ecologists were anxious to develop and explore new approaches that might inform broad-scale issues.

Second, the importance of scale and the development of conceptual frameworks for understanding scale dependence (e.g., Levin 1992) prompted ecologists to examine critically the effect of scale and whether understanding could be translated from one scale to another. The necessity of studies being scaled appropriately for the organism or process of interest was recognized (Addicott et al. 1987, Wiens 1989), and Levin (1992) identified the problem of relating phenomena across scales as the central problem in biology and all of science. Understanding scale has remained closely associated with North American landscape ecology (Miller et al. 2004).

Third, technological advances in computer science, remote sensing, and geographic information systems (GIS) made it possible and affordable to obtain, manipulate and analyze spatial data during the 1980s. Although I do not suggest that the tools drove the science, the increased technical capacity for handling spatial data and models certainly facilitated developments in landscape ecology. Ecologists were able to look at the world through a new lens and to address questions that previously could not have been answered. Collectively, the new questions, technologies and attention to scale fostered the early development of landscape ecology.

The early North American landscape studies shared several common themes, including the focus on scale mentioned above. The role of humans in generating landscape patterns was an early theme, and understanding and predicting human land-use patterns received considerable attention (e.g., Burgess and Sharpe 1981). There also was an understandable initial emphasis on the development and testing landscape metrics because studying the causes and ecological implications of spatial heterogeneity required quantification of spatial pattern. The period of quantitative methods development coincided with the advent of geographic information systems (GIS), but GIS was neither standardized nor widely available to ecologists; most landscape ecologists programmed their spatial analyses directly. Landscape ecologists were also developing methods based on spatial statistics to understand how the magnitude and scale of spatial autocorrelation in a variable of interest differed among landscapes (e.g., Legendre and Fortin 1989). Thus, pattern analysis was a common theme of early landscape studies in North America.

North American landscape ecological studies employed (and still use) an array of approaches because traditional experimental approaches are often impossible to conduct at broad scales. Researchers studied the effects of spatial heterogeneity produced by natural events (e.g., disturbances) and management actions (e.g., forest harvesting; Sirois and Payette 1991, Mladenoff et al. 1993). Retrospective studies using dendrochronology or paleoecological methods revealed how landscapes change in both space and time (e.g., Romme 1982, Delcourt and Delcourt 1988, Arsenault and Payette 1997). Existing variability in landscapes was used to examine the effects of habitat configuration on ecological responses, often in concert with simulation models (e.g., Wegener and Merriam 1979, Henderson et al. 1985). Experimental model systems (EMS) in which small landscapes could be replicated and the responses of small-bodied organisms to alternative spatial structures were evaluated were also implemented (Wiens et al. 1997). Spatially explicit simulation models, in which a much wider range of conditions could be explored, were developed (Baker 1989, Sklar and Costanza 1991, Dunning et al. 1992). These varied modes of inquiry also mirror the four approaches that advance ecological understanding identified by Carpenter (1998): theory and modeling, comparative studies, experimental studies and long-term monitoring.

Despite its rapid growth, landscape ecology encountered resistance from some ecologists in North America. Skepticism focused on the questionable rigor of broad-scale studies, the challenges (and even relevance) of spatially explicit hypothesis testing, issues of pseudo-replication, and a perception that pattern analysis was substituting for science. Indeed, some of these criticisms reflect true challenges that have been met with varying success. The emphasis on quantitative methods development was sometimes esoteric and not always linked to ecological questions. True replication was and still remains problematic for broad-scale studies. The role of spatial heterogeneity may sometimes have been overstated; clearly, it doesn't matter for every ecological study and should be ignored when appropriate. However, progress has been made despite these limits.

The Present: the Focus of Landscape Ecology in North America

What are the current foci of landscape ecology in North America? Landscape ecology studies are now ubiquitous, characterized by a diverse set of basic and applied questions and studies conducted across a wide range of grains and extents. Many quantitative tools are now readily available for characterizing both discrete and continuous representations of spatial heterogeneity (McGarigal and Marks 1995, Gustafson 1998); current research that includes spatial pattern analysis emphasizes appropriate application of methods (e.g., Dorner et al. 2002, Fortin et al. 2003) and how ecological responses or processes are related to pattern (e.g., Jones et al. 2001, Tischendorf 2001). In this section, I identify four general lines of research in contemporary landscape ecology, purposefully grouped to cut across traditional levels of ecological organization and to emphasize the broader conceptual questions. Interested readers might also consult Wu and Hobbs (2002).

Conditions under which spatial pattern must be considered: when does space matter?

Although it is seldom stated so simply, this basic question lies at the heart of many studies that test for the effect of spatial composition or configuration on some ecological response, be it species presence or abundance, the spread of a disturbance or pest, or the delivery of nutrients from a source location to a sink location. Including spatial heterogeneity as either a dependent or independent variable clearly adds a level of complexity to ecological studies. Therefore, knowing when space is going to be influential and when it can be safely ignored remains fundamentally important, both practically and conceptually.

A wide range of theoretical and empirical studies has contributed to current understanding of when space matters. Theoretical studies using neutral landscape models have demonstrated that the influence of spatial configuration varies with habitat abundance (With and King 1997) but may be most important when habitat is of intermediate abundance. Recent studies of the effects of habitat fragmentation suggest that the effects of spatial configuration may be secondary to the effects of habitat loss (Fahrig and Nuttle, *in press*). For populations, Fahrig and Nuttle (*in press*) suggested that configuration will be important if it influences movements of organisms among patches and among-patch movements have a large effect on population survival. Understanding when landscape configuration influences populations remains important for responding to habitat fragmentation (McGarigal and Cushman 2002).

A variety of studies have explored interactions between spatial pattern and disturbance, focusing on whether heterogeneity enhances or retards the spread of disturbance (Turner et al. 1989), and whether some landscape positions are more or less susceptible to disturbance than others. Landscape position or spatial heterogeneity appears to be important when disturbance has a distinct directionality or locational specificity such that some locations are more exposed than others (e.g., Jules et al. 2002). If disturbance has no directionality, landscape position may not have an effect (e.g., Frelich and Lorimer 1991). Current research is extending this research line to consider the interactions of multiple disturbances (e.g., Paine et al. 1998, Bebi et al. 2003).

The effect of spatial pattern on lateral fluxes of matter has also received considerable attention, particularly with regard to the movement of nitrogen and phosphorus from terrestrial land covers to surface waters (e.g., Peterjohn and Correll 1984, Soranno et al. 1996). However, whether just the composition of the uplands (i.e., the amount of different land uses) matters, or if the spatial configuration is also important, remains unresolved because studies have produced conflicting results. Fluxes that move from aquatic to terrestrial systems (e.g., Willson et al. 1998) or between land-cover types (e.g., Seagle 2003) may also be very important.

The influence of landscape context and the scale at which characteristics of the surrounding landscape influence a local response is another way in which the importance of spatial pattern is considered. Effects of landscape context have been demonstrated for a variety of taxa (Mazerolle and Villard 1999) and also for some ecosystem processes (e.g., Gergel et al. 1999). Overall, contemporary landscape research continues to probe the conditions under which spatial pattern must be considered for a wide array of ecological responses.

Understanding spatial dynamics: the linkage of space and time

Understanding and predicting trajectories of landscape change is another important focus of contemporary research in landscape ecology. Paleoecological studies have revealed the dynamic nature of landscapes over long periods. The distributions and abundances of species changed dramatically with climate throughout the Holocene, and some contemporary species assemblages have no past analogs. Major disturbance events (e.g., fires) also catalyzed past shifts in dominant species (Sirois and Payette 1991), and disturbances continue to produce dramatic changes in contemporary landscapes (e.g., Foster et al. 1998). North American landscapes also changed profoundly in response to Euro-American settlement. Landscape ecologists seek to understand and predict changes in landscape structure and function through time in response to a variety of drivers including climate, natural disturbances and land use.

Studies of how landscapes change through time in response to natural disturbances have included management implications of historical range of variability (Landres et al. 1999) and extension of equilibrium concepts. Considerable attention has focused on the potential of natural disturbance regimes serving as a model for the spatial pattern and timing of human disturbances (e.g., Hunter 1993). The scale-dependent nature of equilibrium (Perry 2002) was elucidated—equilibrium conditions may be observed at some scales of space and time, but nonequilibrium conditions are also common and may even be prevalent.

Explaining and predicting patterns of land-use change is an important topic that links space and time and also underscores the role interdisciplinary studies. For example, in forested landscapes of the interior Columbia Basin, the social system constrained the influence of the biophysical factors on landscape changes (Black et al. 2003). Land ownership systems, economic market structure, and cultural value systems dominated changes in this landscape (Black et al. 2003). Understanding the spatiotemporal dynamics of many landscapes requires understanding the drivers of human land use.

The potential importance of historical legacies for contemporary species assemblages and landscape function is another way in which spatial and temporal dynamics are linked; the past continues to influence the present. Natural disturbances can produce enduring legacies of physical and biological structure that influence ecosystem processes for decades or centuries (e.g., Foster et al. 1998). Similarly, patterns of historical land use can influence contemporary forest composition and ecosystem processes for a very long time (Dupouey et al. 2002). Understanding how landscapes change through time, including the long-term legacies of past disturbance or land use, is an important line of inquiry in contemporary landscape ecology.

Nonlinearities and thresholds: expecting the unexpected

Understanding nonlinear dynamics or thresholds and how they influence landscape function is important because outcomes may be unexpected (Groffman et al., *in press*). 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., *in press*). Landscape analyses based on percolation theory and neutral landscape models (With and King 1997) have suggested the importance of critical thresholds in habitat abundance above or below which ecological processes are qualitatively different. The numerical value of critical thresholds depends on the particular process and landscape, but the occurrence of the threshold does not (With and King 1997). Below the thresholds, patches are small and isolated; above the threshold, patches are large and well connected. Changes in habitat abundance that occur near the critical threshold may produce large, surprising changes in the system because the habitat can suddenly become connected or disconnected. Empirical studies support the existence of critical thresholds in habitat abundance for bird and mammal populations (Andren 1994). The spatial spread of disturbances such as fire may also exhibit threshold responses related to habitat abundance (Turner et al. 1989).

Thresholds can occur in a range of variables related to landscape pattern. For example, some organisms require patches of a minimum size for persistence, although the generality of this has been debated (Bowers and Matter 1997). Patch size and shape influence the ability of animals to persist in a landscape and may show threshold effects (Lindenmeyer et al. 1999), and patch size influences nutrient dynamics in nonlinear ways (Ludwig et al. 2000). Thresholds for land-use indicators (impervious surface, agricultural land use, lake shore development) and ecosystem services (fish communities, coarse woody debris, stream nitrate concentrations) have also been suggested. For example, Paul and Meyer (2001) suggested a threshold of 10–20% impervious surface for maintaining stream ecosystem integrity in developed watersheds, and active tests of this metric are underway. Not exceeding a threshold of 50% agricultural land in a watershed has been suggested as critical for the maintenance of fish communities in Wisconsin streams (Wang et al. 1997). When considered in the context of landscapes changing through time, the identification of nonlinear relationships and threshold dynamics takes on particular importance. Identifying nonlinearites related to spatial patterns and ecological responses remains a consistent theme in landscape studies.

Planning, managing, and restoring landscapes

Demand for the scientific underpinnings of managing landscapes and incorporating the consequences of spatial heterogeneity into land management is substantial (Perera et al. 2000, Liu and Taylor 2002). As the ecological science that focuses on spatial dynamics, landscape ecology has been part of the discussions of how alternative spatial arrangements of land cover or land use may influence ecological functions. Identifying an optimal landscape configuration may be impossible, as the optimal arrangement will depend on specific management objectives that may conflict with one another. Nonetheless, land management decisions are made, and landscape ecology should be at the table. Landscape studies have quantified relationships between landscape features and changes in land use and land cover (e.g., Black et al. 2003), and recent studies have explored the ecological implications of low-density residential development that may be "under the canopy" (e.g., Miller et al. 2003). Residential development has replaced agricultural and extractive uses in many rural areas (Hansen et al. 2002), yet the ecological implications of such development are poorly understood.

Landscape studies have also addressed questions of ecological restoration (e.g., Palik et al. 2000). Application of a landscape perspective augments restoration approaches based on community composition by considering dynamic reference states and the spatial configuration of communities. Without this perspective, restoration may lack the spatial and historical context needed for success. Landscape ecology can and should contribute to land planning, management, and restoration.

The Future: What Lies Ahead?

Landscape ecology has already influenced North American ecology; explicitly accounting for spatial pattern and recognizing the influences of scale are likely here to stay. An informed decision about whether or not to consider spatial heterogeneity is now pro forma. Contemporary landscape ecology studies are conducted over a wide range of spatial scales, not only in large areas. Terrestrial studies predominate, but landscape ecology studies are not limited to the land. The interplay between models, theory and empirical data is a hallmark of landscape ecology in North America. Wherein lie the key future research questions and directions? Here, I suggest several areas that are not yet well developed in landscape ecology and where there may be opportunities for substantial progress.

Broader representations of spatial heterogeneity

How spatial heterogeneity is conceptualized and then put into practice needs to be broadened. Categorical maps and point data are the most common representations of spatial heterogeneity (Gustafson 1998). Discrete space has often been used as a simplifying assumption, and indeed, much has been learned from this. However, many variables of ecological interest are continuous (e.g., ecosystem process rates), and gradients abound in many of the variables used as predictors (e.g., leaf area index). Habitat suitability for a particular organism is another attribute that can vary continuously. The conceptual framework for understanding spatial heterogeneity must be extended beyond a patch-based view to include both discrete and continuous representations of space, and furthermore, to account for their changes through time.

Spatial heterogeneity in ecosystem function

Understanding the patterns, causes, and consequences of spatial heterogeneity for ecosystem function is a research frontier in both landscape ecology and ecosystem ecology (Lovett et al. 2005). Progress at the interface of ecosystem and landscape ecology has been relatively slow compared to other areas, yet spatial fluxes of matter, energy and information influence the functioning of individual ecosystems and heterogeneous landscapes. Spatial heterogeneity can affect both the drivers of ecosystem processes, which are often multivariate, as well as in the pools or flux rates that are often response variables. Integrating the understanding gained from ecosystem and landscape ecology would enhance progress in both disciplines while generating new insights into how landscapes function.

Spatial cascades

The influence of spatial heterogeneity on interactions among species (rather than on individual populations) also represents an important future research direction. Much of the research on how spatial pattern affects organisms focuses on how variables like patch size, edge-to-area ratio, and interpatch distances influence population presence or abundance, largely through effects on key demographic parameters. However, some changes in landscape patterns may have cascading influences among species (Tallmon et al. 2003), and more work is needed on how spatial heterogeneity affects species interactions.

Integrating new technologies and fields

New technologies and analytical capabilities offer considerable promise for expanding the empirical foundation of landscape ecology. For example, molecular population genetics has been integrated with landscape ecology to explain observed spatial genetic patterns (e.g., clines, isolation by distance, genetic boundaries to gene flow, metapopulations) with landscape variables (Manel et al. 2003). For mobile animals, the use of radiocollars with on-board global positioning systems (GPS) is providing new data on movement and habitat use at finer spatial and temporal resolution (e.g., Johnson et al. 2002). The growing array of earth observing sensors offers the ability to sense more functional response variables for both the land surface and vegetation (e.g., canopy foliar nitrogen concentrations; Smith et al. 2002). These methods have great promise for extending landscape studies to three dimensions, e.g., by incorporating vertical structure in terrestrial and aquatic systems. New sampling designs derived from spatial statistics are being used to sample across multiple scales, providing new insights about spatial variation (e.g., Burrows et al. 2002, Fraterrigo et al. 2005). Spatial extrapolations based on simulation or statistical models can be used as powerful tests of the mechanisms underlying relationships between pattern and process (Miller et al. 2004). While all these advancements hold great promise, it is nonetheless important to remember that spatially extensive measurement of many ecological processes remains a formidable challenge.

Conclusion

Landscape ecology has influenced how ecologists view the world; its central theme of understanding the causes and ecological consequences of spatial heterogeneity has been widely embraced. Should landscape ecology of the future retain its distinctive identity? Does landscape ecology have sufficient theory and novel ideas to maintain separateness? Or, is landscape ecology an interdisciplinary or transdisciplinary science? I suggest that a landscape ecological perspective has brought a unique set of questions and approaches to ecology, and as such, it has developed an identity that is useful to maintain. However, landscape ecological concepts and methods are now used regularly in many ecological subdisciplines, and perhaps this widespread incorporation of landscape ecology concepts and methods should be viewed as a mark of success irrespective of whether the "landscape ecology" moniker is invoked. Landscape ecology should continue to push the limits of understanding of the reciprocal interactions between spatial patterns and ecological processes and seek opportunities to test the generality of its concepts across systems and scales.

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