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Spatial heterogeneity and ecosystem processes

4.1 Introduction

Understanding the patterns, causes, and consequences of spatial heterogeneity for ecosystem function is a research frontier in both landscape ecology and ecosystem ecology (Turner *et al.* 2001, Chapin *et al.* 2002, Wu and Hobbs 2002, Lovett *et al.* 2005). Landscape ecology research has contributed to tremendous gains in understanding the causes and consequences of spatial heterogeneity, how relationships between patterns and processes change with scale, and the management of both natural and human-dominated landscapes. There are now many studies in widely varied landscapes that elucidate, for example, the conditions under which organisms may respond to landscape composition or configuration, or disturbance spread may be constrained or enhanced by landscape pattern. The inclusion of a spatial component is now pro forma in many ecological studies, and tools developed by landscape ecologists for spatial analysis and modeling now enjoy widespread use (e.g., Baskent and Jordan 1995, McGarigal and Marks 1995, Gustafson 1998, Gergel and Turner 2002). Landscape ecological approaches are not limited only to "land" but are also applied in aquatic and marine ecosystems (e.g., Fonseca and Bell 1998; Bell *et al.* 1999; Garrabou *et al.* 2002; Teixido *et al.* 2002; Ward *et al.* 2002). However, with a few exceptions, the consideration of ecosystem function has lagged behind progress in understanding the causes and consequences of spatial heterogeneity for other ecological processes.

Ecosystem ecology focuses on the flow of energy and matter through organisms and their surroundings, seeking to understand pools, fluxes, and regulating factors. From its initial descriptions of how different ecosystems (e.g., forests, grasslands, lakes and streams) vary in structure and function,

Key Topics in Landscape Ecology, ed. J. Wu and R. Hobbs.
Published by Cambridge University Press.

ecosystem ecology moved toward quite sophisticated analyses of function – e.g., food web analyses, biogeochemistry, regulation of productivity, and so on (Golley 1993, Pace and Groffman 1998, Chapin *et al.* 2002). However, ecosystem ecology has typically emphasized understanding changes through time within a single ecosystem rather than understanding variation across space (but see Ryszkowski *et al.* 1999). Recent studies suggest that spatial variability in some ecosystem processes may be of similar magnitude to temporal variation (e.g., Burrows *et al.* 2002, Turner *et al.* 2004), and efforts to explain and predict such variation are increasing. The importance of transfers among patches, representing losses from donor ecosystems and subsidies to recipient ecosystems, for the long-term sustainability of ecosystems is also now acknowledged explicitly (Naiman 1996, Carpenter *et al.* 1999, Chapin *et al.* 2002). Ecosystem studies have elucidated the mechanisms underlying temporal dynamics of many processes, but there has been comparatively little explicit treatment of spatial heterogeneity.

Progress at the interface of ecosystem and landscape ecology has been relatively slow, despite a tradition in Eastern Europe (e.g., Ryszkowski and Kedziora 1993, Ryszkowski *et al.* 1999) and stronger connections during the early development of landscape ecology in North America (e.g., Risser *et al.* 1984, Gosz 1986). Integration of the understanding gained from ecosystem and landscape ecology would likely enhance progress in both disciplines while generating new insights into how landscapes function. Indeed, gaining a more functional understanding of landscapes is a goal shared by ecosystem and landscape ecology. In this chapter, we identify key questions that could guide a research agenda in spatial heterogeneity and ecosystem function, focusing on four key research areas in which significant progress can be made: (1) understanding spatial heterogeneity of process rates, (2) land-use legacies, (3) lateral fluxes in landscape mosaics, and (4) linking species and ecosystems.

4.2 Understanding the spatial heterogeneity of process rates

Understanding variability in the rates of key ecosystem processes is a major focus of ecosystem ecology (Chapin *et al.* 2002). “Point processes” are those that can be well represented by rates measured at a particular location in space and time (Turner and Chapin 2005), and for these processes, spatial variation among replicate measurements is often averaged to estimate a mean value. For example, net primary production, net ecosystem production, denitrification, and nitrogen mineralization are processes understood in many systems using methods of analysis focused on spatially independent measurements. Most ecosystem ecologists have focused on understanding the mean rates and their temporal dynamics, in spite of the “noise” owing to spatial variation.

However, the basic causes of spatial heterogeneity in point-process rates have been well known for a long time (Jenny 1941). Heterogeneity is derived from the abiotic template, including factors such as climate, topography, and substrate. In addition, ecosystem process rates may vary with the biotic assemblage, disturbance events (including long-term legacies), and the activities of humans (Chapin *et al.* 1996, Amundson and Jenny 1997). Despite the acknowledgement of sources of spatial heterogeneity, there has been relatively little empirical work designed to characterize the spatial variation of process rates, the spatial scales over which variation is manifest, and the factors that control such variation.

Recent studies have demonstrated that understanding temporal behavior in mean rates may not be adequate; understanding spatial variance in process rates may lead to new insights into the mechanisms governing ecosystem dynamics and new approaches for predicting landscape function (van Dokkum *et al.* 2002, Beneditti-Cecchi 2003). Understanding the locations and direct and indirect effects of the spatial and temporal variation in process rates across landscapes could help reveal the relative importance of abiotic, biotic, and human factors, which interact across potentially different scales of time and space to both constrain and produce observed spatial pattern.

Studies linking disturbance, succession, and ecosystem processes in Yellowstone National Park illustrate how new insights and predictive power can be gained from understanding variation in process rates (Turner *et al.* 1994, 1997, 2004). The 1988 Yellowstone fires created a landscape mosaic in which post-fire lodgepole pine densities varied from 0 to $>500\,000$ stems ha^{-1}. This spatial heterogeneity in sapling density resulted largely from contingencies such as the spatial variation in fire severity and in pre-fire serotiny within the stand, rather than from the abiotic template. The tremendous variation in stand density in turn generated substantial heterogeneity in aboveground net primary production (ANPP), which ranged from 1 to 15 Mg ha^{-1} yr^{-1} ten years after the fires (Turner *et al.* 2004). Analyses of how spatial variation in stand density and growth rate (basal area increment, an index of ANPP) changes with stand age revealed that effects of the initial post-fire mosaic persists for at least a century (Kashian 2002, Kashian *et al.* 2005). Had only mean ANPP been studied and the spatial variability in ANPP ignored, it is likely that key factors influencing the process would not have been identified.

Understanding the spatial patterns of ecosystem process rates is also fundamental to spatial extrapolation over large areas. Obtaining field measurements of many ecosystem process rates across large areas is costly, and relatively few spatially extensive empirical data sets exist. Remote sensing methods and platforms offer promise for some variables on land (Groffman and Turner 1995, Martin and Aber 1997, Serrano *et al.* 2002), in wetlands (Urban *et al.* 1993), and in the open ocean (Karl 2002). Extrapolation of process rates across heterogeneous landscapes using empirical data or simulation models combined with GIS data layers can be used to test hypotheses about the influence of independent variables (Miller *et al.* 2004). Running *et al.* (1989) were among the first to integrate biophysical data obtained from many sources and combine these data with an ecosystem simulation model to predict evapotranspiration, leaf-area index and net photosynthesis across a large landscape. Their estimates 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). Empirical extrapolations combined with GIS data have been used to predict rates of denitrification in southern Michigan (Groffman *et al.* 1992), net nitrogen mineralization within forests of the Midwestern Great Lakes region (Fan *et al.* 1998), and aboveground net primary production in western Yellowstone National Park (Hansen *et al.* 2000). Using spatial extrapolation in a hypothesis-testing mode represents a powerful approach that could be used much more widely in studies of spatial heterogeneity of point-process rates (Miller *et al.* 2004).

A first research priority for linking ecosystem and landscape ecology should focus on understanding the spatial structure of variation in rates at multiple scales, the factors that produce the spatial variation, and the consequences of that variation for other ecological phenomena (Table 4.1). Methods from landscape ecology that consider both continuous and discrete representations of spatial data should be integrated with studies of ecosystem processes to build understanding of landscape function.

4.3 Influence of land-use legacies

Landscape ecology has made important contributions to our understanding of land-use change, including the natural and socioeconomic drivers of land-use change, how it affects landscape structure, and how organisms may respond. Recent studies have documented the importance of historical land use in explaining contemporary ecosystems and landscapes (Foster *et al.* 2003). For example, historical land use influences current vegetation composition in New England forests (Currie and Nadelhoffer 2002, Foster 2002, Hall *et al.* 2002, Eberhardt *et al.* 2003). Comparisons of formerly cultivated forests with reference forests in North America and Europe suggest that agricultural practices can alter soil nutrient content and net nitrification rates for at least a century after abandonment (Koerner *et al.* 1999, Compton and Boone 2000, Goodale and Aber 2001, Dupouey *et al.* 2002, Jussy *et al.* 2002). Thus, historical patterns of land use may be important drivers of the pattern and variability in current

TABLE 4.1. *Suggested general questions that could guide research in each of four areas in which progress is both needed and possible at the interface of landscape ecology and ecosystem ecology*

Topic area	Research questions
Spatial heterogeneity of process rates	• How spatially heterogeneous are ecosystem process rates? • What causes variation in ecosystem process rates? • What are the consequences of variation in process rates on key ecological phenomena?
Influence of land-use legacies	• What is the role of land-use legacies in explaining the state of contemporary ecosystems? • How persistent are the effects of historical land use?
Lateral fluxes in landscape mosaics	• In landscape mosaics, how does spatial configuration influence pools and lateral fluxes of matter, energy and information? • What are the relative roles of spatial variation in initial conditions, local process rates, and lateral connections for pools and fluxes? • How do effects of spatial heterogeneity differ in one-way networks and mosaics with multidirectional flows?
Linking species and ecosystems	• How do trophic cascades influence vegetation mosaics and rates of ecosystem processes? • How do the spatial movements of organisms respond to and create spatial heterogeneity in ecosystem process rates?

rates of ecosystem processes. Landscape ecologists have often conducted studies that quantify how landscape patterns have changed through time; however, in few cases have linkages been made between historical landscapes, their trajectories, and the ecosystem processes.

Understanding the functional role of land-use legacies could be addressed by combining the spatial analysis methods of landscape ecology with the process-based approach of ecosystem ecology. Landscape ecology offers sophisticated methods to quantify land-use patterns as they change through time. This information could be used to stratify field sampling locations by historical land use and other appropriate variables, such as factors that relate to the abiotic template (e.g., elevation, slope, aspect, substrate). Pools and process rates for key functional variables can be measured using traditional methods from ecosystem ecology (e.g., Sala *et al.* 2000). Spatial extrapolation can again serve as a means of testing the predictive power of current understanding, and also of identifying locations in a landscape where some pool or flux of interest may be especially high or low.

The use of new quantitative methods that consider the magnitude and scale of spatial variability in ecosystem response variables may also yield important new insights. Ecosystem processes are usually measured as continuous rather than categorical variables, and methods derived from spatial statistics are ideally suited for studying spatial variation in continuous data. Many of these methods (e.g., semivariograms, correlograms, kriging) are similar to time-series analyses that identify temporal periodicities in a data set. Spatial statistics also provide guidance for efficient sampling schemes to assess the spatial structure of continuous data (e.g., Burrows *et al.* 2002, Fraterrigo *et al.* in review).

Understanding the influence of historical land-use patterns on vegetation and soils in the Southern Appalachian Mountains illustrates how a blending of landscape and ecosystem ecology can be used to understand the effects of historical land use on landscape function. Spatial-pattern analyses of these landscapes have identified topographic positions and forest communities that have been influenced by land-use changes to a greater or lesser degree (e.g., Wear and Bolstad 1998, Turner *et al.* 2003). Historical land use has strongly affected mesic forest communities and the occurrence and abundance of herbaceous plants within these forests (Duffy and Meier 1992; Pearson *et al.* 1998, Mitchell *et al.* 2002, Turner *et al.* 2003). However, the long-term (> 50 yr) impacts of land use on the spatial heterogeneity of soil nutrients are poorly understood. Fraterrigo *et al.* (in review) examined patterns of nutrient heterogeneity in the mineral soil (0–15 cm depth) of 13 southern Appalachian forest stands in western North Carolina > 60 yr after abandonment from pasture or timber harvest using a cyclic sampling design derived from spatial statistics. Mean concentrations rarely indicated an enduring effect of historical land use on nutrient pools, but the spatial heterogeneity of nutrient pools differed substantially with past land use. Nutrient pools were most variable in reference stands, and this variability was greatest at fine scales. In contrast, formerly pastured and logged stands generally exhibited less variability, and soil nutrients were relatively more variable at coarse spatial scales. Geostatistical analysis of fine-scale patterns further revealed that spatial structure of soil cations was more closely linked to former land use than observed for other soil nutrients. These results suggest that land use has persistent effects on the spatial heterogeneity of soil resources, which may not be detectable when values are averaged across sites (Fraterrigo *et al.* in review). These insights were only possible by combining the spatial approaches of landscape ecology with the analytical methods of ecosystem ecology.

All landscapes exist and change in a framework of both natural and cultural legacies. Historical natural disturbances such as fire, floods, and storms appear to strongly influence contemporary systems, and analysis of cultural history of contemporary landscapes has assumed greater importance in recent decades (Foster *et al.* 2003). Yet studies of the impact of prior historical conditions of a landscape are relatively few. Landscape ecology can contribute by linking a temporally extended understanding of landscape spatial dynamics with functional measurements and the application of methods for analyzing continuous data. We suggest a second research priority for linking landscape and ecosystem ecology directed toward understanding the relative importance of historical landscape conditions for explaining contemporary ecosystem dynamics, along with quantifying the persistence time of legacy effects on different ecosystem characteristics and processes (Table 4.1).

4.4 Lateral fluxes in landscape mosaics

Lateral fluxes of matter, energy or information in spatially heterogeneous systems have been recognized as key foci within landscape ecology in particular (Risser *et al.* 1984, Wiens *et al.* 1985, Turner *et al.* 1989, Shaver *et al.* 1991) and ecology in general (e.g., Reiners and Driese 2001). Broad conceptual frameworks have considered the conditions under which spatial pattern, or particular aspects of spatial pattern, should influence a lateral flux. For example, Wiens *et al.* (1985) proposed a framework for considering fluxes across boundaries that included the factors determining the location of boundaries between patch types in a landscape mosaic, how boundaries affect ecological processes and the movement of materials over an area, and how imbalances in these transfers in space can affect landscape configuration. Weller *et al.* (1998) explored how and why different riparian buffer configurations would vary in their ability to intercept nutrient fluxes moving from a source ecosystem to an aquatic system. Simulation models ranging from simple representations (e.g., Gardner *et al.* 1989, Turner *et al.* 1989, Gardner *et al.* 1992) to complex, process-based spatial models (e.g., Costanza *et al.* 1990, Sklar and Costanza 1990, Fitz *et al.* 1996) have also been employed to identify the aspects of spatial configuration that could enhance or retard a lateral flux. However, a general understanding of lateral fluxes in landscape mosaics has remained elusive, despite promising conceptual frameworks developed for semi-arid systems (e.g., Tongway and Ludwig 2001).

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 (Correll *et al.* 1992, Hunsaker and Levine 1995). Most of these studies focus on nutrients, such as nitrogen or phosphorus, related to eutrophication of surface waters (e.g., Lowrance *et al.* 1984, Peterjohn and Correll 1984, Soranno *et al.* 1996, Jordan *et al.* 1997, Bennett *et al.* 1999). For example, in a recent study of the US Mid-Atlantic region, landscape heterogeneity explained from 65–86 percent of the variation in nitrogen yields to streams (Jones *et al.* 2001). 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 absence of mechanistic understanding about how materials actually flow horizontally across heterogeneous landscapes.

The insights to be gained by focusing on the pathways of lateral fluxes are exemplified by studies of nitrogen retention in Sycamore Creek, Arizona focusing on hydrologic flowpaths as functional integrators of spatial heterogeneity in streams (Fisher and Welter 2005). Building upon a long history of research on this desert stream, Fisher and Welter found that nitrogen retention of the whole system could not be predicted simply by summing the rates observed in system components; rather, the lateral transfers through spatially heterogeneous space had to be understood explicitly. In particular, the geometry of different patches, such as sand bars, that influenced nitrogen processing was critical to understanding nitrogen transport and retention.

Understanding surface- and groundwater fluxes among lake chains in northern Wisconsin has demonstrated the importance of lateral fluxes for lakes. A lake's landscape position is described by its hydrologic position within the local to regional flow system and the relative spatial placement of neighboring lakes within a landscape (Webster *et al.* 1996, Kratz *et al.* 1997, Riera *et al.* 2000). Many hydrologic and biological properties of a lake are determined directly by landscape position, which reflects the relative contributions of surface- and groundwater to the lake (Kratz *et al.* 1997, Soranno *et al.* 1999, Riera *et al.* 2000). Yet across large areas (e.g., an entire lake district containing thousands of lakes), surface- and groundwater connections among lakes are not well understood, making it difficult to predict the function of individual lakes that have not been intensively studied or of the integrated land–water mosaic.

Approaches from landscape ecology could contribute to general understanding of the influence of spatial structure on stocks and fluxes across space. For example, measures of composition and configuration could be adapted to the node-and-link structure of systems with lateral fluxes. Spatial models that track the movement of organisms or propagules might be considered for applicability to matter and energy. Furthermore, only a small subset of the lateral transfers of matter, energy, and information across landscape mosaics has been studied. There is a tremendous opportunity to seek a general understanding of lateral transfers in heterogeneous landscapes. We suggest that landscape ecologists extend their frameworks and approaches for the reciprocal interactions between pattern and process to the realm of fluxes of matter, energy, and information. Priorities should focus on understanding the importance of spatial configuration of fluxes, the relative importance of controlling factors, differences between uni- and multidirectional flows, and the role of disturbance (Table 4.1).

4.5 Linking species and ecosystems

Strengthening the ties between species and ecosystems, between population ecology and ecosystem ecology, has been recognized as an important disciplinary bridge within ecology (e.g., Jones and Lawton 1995). Organisms exist in heterogeneous space; they also use, transform, and transport matter and energy. The importance of herbivores in redistributing nutrients across landscapes has been recognized for some time. For example, grazers can enhance mineral availability by increasing nutrient cycling in patches of their waste (McNaughton *et al.* 1988, Day and Detling 1990, Holland *et al.* 1992). The cascading influence of herbivores on nutrient cycling through their modification of plant community composition has also been recognized (e.g., McInnes *et al.* 1992, Pastor *et al.* 1997). Recent studies have also identified the role of piscivores in transporting nutrients derived from aquatic ecosystems to terrestrial ecosystems through their foraging patterns (e.g., Willson *et al.* 1998, Helfield and Naiman 2002, Naiman *et al.* 2002). Considering habitat use and movement patterns of species in a spatial context provides a wealth of opportunities to enhance the linkage between species and ecosystems and again enhance functional understanding of landscape mosaics.

Recent studies have identified the importance for vegetation patterns of spatial heterogeneity in trophic cascades. For example, in the western US, extirpation of wolves in the twentieth century has been linked to increased ungulate population sizes and high rates of herbivory on woody plants such as aspen (*Populus tremuloides*) and willow (*Salix* spp.) (e.g., Romme *et al.* 1995, Ripple and Larsen 2000, Berger *et al.* 2001, Beschta 2003). With predator restoration in some North American national parks, numerical or behavioral responses of ungulates to predators may lead to spatial heterogeneity in browsing and possibly the recovery of woody vegetation in some locations on the landscape (White *et al.* 1998, Ripple *et al.* 2001, National Research Council 2002, Ripple and Beschta 2003). Such trophic cascades, when played out spatially in dynamic landscapes, may have important implications for dynamics of the vegetation mosaic. In tropical forest fragments, predator elimination has also been associated with increased herbivore abundance and a severe reduction in seedlings and saplings of canopy tree species (Terborgh *et al.* 2001).

Large herbivores are known to respond to spatial heterogeneity in the distribution of forage resources, but how important herbivores are in creating those spatial patterns, how their influence may be scale dependent, and how herbivore-induced patterns affect ecosystem processes remain unclear (Augustine and Frank 2001). Herbivore-mediated changes in forest composition have been shown to have important implications for patterns of nutrient cycling (Pastor *et al.* 1998, 1999). In Isle Royale National Park, selective browsing by moose (*Alces alces*) altered forest community composition which, in turn, changed nutrient cycling rates in the soil. Augustine and Frank (2001) demonstrated an influence of grazers on the distribution of soil N properties at every spatial scale from individual plants to landscapes. These studies suggest that much may be learned through integrative studies of population dynamics and ecosystem processes.

Taking a landscape perspective in which the linkages between species and ecosystems play out in space offers an unprecedented opportunity to enhance the linkages between these traditionally separate sub-disciplines within ecology. Populations both respond to and create heterogeneity in their environments; ecosystem processes, similarly, can both influence species' patterns of occurrence and behaviors and also respond to biota. Population/community and ecosystem ecologists have historically asked quite different research questions. We suggest that the landscape ecology may provide the conceptual framework through its emphasis on spatially explicit studies to integrate populations and ecosystems much more effectively (Table 4.1).

4.6 Concluding comments

The successful integration of ecosystem ecology and landscape ecology should produce a much more complete understanding of landscape function than has been developed to date. We have identified four areas in which progress is both important and possible: understanding the causes and consequences of spatial heterogeneity in ecosystem process rates; the influence of land-use legacies on current ecosystem condition; horizontal flows of matter and energy in landscape mosaics; and the linkage between species and ecosystems.

Achieving this integration will require progress in several areas. First, continuous and categorical conceptualizations of space must be used in much more complimentary ways (Gustafson 1998). Discrete or patch-based representations of spatial heterogeneity dominate in landscape ecology, yet ecosystem ecology is often characterized by continuous variation in pools or fluxes. Second, models and empirical studies both must be brought to bear on questions of how spatially heterogeneous landscapes both create and respond to fluxes of matter, energy, and information. Studies that encompass broad spatial extents remain logistically difficult; while this is stating the obvious, it is important to recognize that studying ecosystem processes in large and heterogenous areas remains a nontrivial challenge. Third, landscape and ecosystem ecologists should collaborate to explore new technologies that may facilitate spatially extensive measurements. Landscape-ecosystem ecologists should be proactive, describing the measurements that are highly desirable but not yet technologically feasible at particular spatial–temporal scales. Fourth, collaborative research should be the rule rather than the exception. Most scientists do not have the training in all aspects of the science required to address the research questions we have identified – e.g., understanding spatial analysis, landscape patterns, and their change through time; knowing all the field and analytical procedures for ecosystem process measurements; spatial statistics; microbial ecology; and modeling. Effective collaborations may be requisite for progress.

Understanding the implications of the dynamic landscape mosaic for ecosystem processes remains a frontier in ecosystem and landscape ecology. The potential benefits of integrating landscape and ecosystem ecology are important for landscape management and ecological restoration. Maintenance of ecosystem services in changing landscapes has been identified as a key priority for resource management from local to global scales (e.g., Daly 1997, Naiman and Turner 2000, Amundson *et al.* 2003, Loreau *et al.* 2003, Schmitz *et al.* 2003). Clearly, achieving this goal requires a much greater functional understanding of landscapes than is currently available. Landscape ecology offers tremendous promise for providing a conceptual framework to understand reciprocal interactions between spatial heterogeneity and ecosystem processes. We challenge landscape ecologists to embrace the functional complexity of ecosystem ecology, and ecosystem ecologists to similarly embrace the spatial complexity of their systems.

Acknowledgments

We thank Jianguo Wu and Richard Hobbs for the invitation to participate in the symposium at the IALE World Congress in Darwin, Australia, and for partial support for travel to that conference. We also acknowledge funding for this work from the National Science Foundation and the Andrew W. Mellon Foundation.

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