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LANDSCAPE ECOLOGY: What Is the State of the Science?

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■ **Abstract** Landscape ecology focuses on the reciprocal interactions between spatial pattern and ecological processes, and it is well integrated with ecology. The field has grown rapidly over the past 15 years. The persistent influence of land-use history and natural disturbance on contemporary ecosystems has become apparent. Development of pattern metrics has largely stabilized, and they are widely used to relate landscape pattern to ecological responses. Analyses conducted at multiple scales have demonstrated the importance of landscape pattern for many taxa, and spatially mediated interspecific interactions are receiving increased attention. Disturbance remains prominent in landscape studies, and current research is addressing disturbance interactions. Integration of ecosystem and landscape ecology remains challenging but should enhance understanding of landscape function. Landscape ecology should continue to refine knowledge of when spatial heterogeneity is fundamentally important, rigorously test the generality of its concepts, and develop a more mechanistic understanding of the relationships between pattern and process.

INTRODUCTION

Scientists have observed and described heterogeneity (complexity or variability in a system property of interest in space and time) (Li & Reynolds 1995) in ecological systems for a very long time. However, an explicit focus on understanding spatial heterogeneity—revealing its myriad abiotic and biotic causes and its ecological consequences—emerged in the 1980s as landscape ecology developed and spatial data and analysis methods became more widely available. Since then, progress in landscape ecology has been substantial and rapid, and its concepts and methods are now widely used in many branches of ecology. Landscape ecological approaches are not limited to land, but are also applied in aquatic and marine ecosystems (e.g., Bell et al. 1999, Ward et al. 2002). Research in landscape ecology has enhanced understanding of the causes and consequences of spatial heterogeneity and how they vary with scale and has influenced management of both natural and human-dominated landscapes.

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Most generally, a landscape is an area that is spatially heterogeneous in at least one factor of interest (Turner et al. 2001). This flexible definition is applicable across scales and adaptable to different systems. Landscape ecology, a term coined by the German biogeographer Carl Troll and elaborated in 1950 (Troll 1950), arose from the European traditions of regional geography and vegetation science and was motivated by the new perspective offered by aerial photography. Landscape ecology has since been defined in various ways (Pickett & Cadenasso 1995, Risser et al. 1984, Turner 1989, Turner et al. 2001, Urban et al. 1987), but common to all definitions is a focus on understanding the reciprocal interactions between spatial heterogeneity and ecological processes. Nonetheless, landscape ecology has developed with two distinct approaches that, although not mutually exclusive, have led to some confusion about its scope. Landscape ecology often emphasizes large areas or regions and includes humans and their activities, which reflects a strong European tradition. The focus of landscape ecology is more anthropocentric in Europe and aligned closely with land planning (e.g., Bastian 2001, Opdam et al. 2002). However, landscape ecology also encompasses the causes and consequences of spatial pattern at variable spatial scales defined by the organism or process of interest, which reflects traditions in North America and Australia. Thus, streambeds may be considered landscapes for stream invertebrates (Palmer et al. 2000), and spatial heterogeneity in soils may be characterized at very fine scales relevant to individual plants or even microbes. These diversities in approach and tradition are both contrasting and complimentary (Wu & Hobbs 2002) and an inherent part of the field.

The rapid development of landscape ecology in the past two decades suggests that a review of the field is timely, albeit daunting. The number of landscape ecology articles published each year has increased exponentially since the early 1990s (Turner 2005). Reviews have been published for particular areas of landscape ecology, such as quantitative analyses of spatial pattern (e.g., Gustafson 1998, Haines-Young & Chopping 1996, Hargis et al. 1998, Li & Reynolds 1995) and disturbance dynamics (e.g., Foster et al. 1998, Perry 2002), and several synthetic articles have catalyzed progress (e.g., Pickett & Cadenasso 1995, Wiens 1999, Wu & Hobbs 2002). An edited volume of early foundation papers in landscape ecology provides access to the intellectual foundations of the field and lists the numerous books on landscape ecology published in the past decade (Wiens et al. 2005). Here, I emphasize developments in landscape ecology since my 1989 review (Turner 1989) and use a similar organization for context and comparison. My focus is primarily on contributions of landscape ecology to basic ecological understanding rather than to land management. I identify general concepts, highlight contemporary areas of inquiry, and suggest future research directions.

Several general themes are implicit throughout this review. First, understanding scale (Levin 1992, Wiens 1989) has been and remains closely aligned with landscape ecology. As ecology moved to broader scales and embraced heterogeneity, an understanding of the profound effects of grain, extent, and level of organization on analyses was crucial. Second, landscape ecology addresses both basic and applied questions and moves easily between these realms; indeed, the demand for landscape science in resource management has been quite high (Liu & Taylor 2002). Third, the use of multiple approaches, including historical or remotely sensed data, field measurements, experimental model systems, and simulation modeling, is the norm in landscape studies; the interplay of models and data has been characteristic of the field.

CAUSES OF LANDSCAPE PATTERN

Landscape patterns result from complex relationships among multiple factors, many of which are well known. The abiotic template includes climate, which strongly controls biogeographic patterns, and landform, which produces patterns of physical relief and soil development (e.g., Parker & Bendix 1996). Biotic interactions—such as competition, herbivory, and predation—and the role of keystone species or ecosystem engineers are played out on the abiotic template and influence species assemblages. Disturbance and succession are key drivers of spatial and temporal heterogeneity; many disturbances have a strong climate forcing and may interact with landform. Finally, the ways in which humans use the land are key drivers of landscape pattern (Riitters et al. 2002). These causes have been well described for many systems, yet explaining and predicting landscape patterns remains surprisingly difficult. Current questions focus on understanding landscape legacies and multiple drivers and their interactions, and on forecasting future landscapes.

Landscape Legacies

What aspects of current landscape patterns are explained by past land use or disturbance, and for how long do such influences persist? All landscapes have a history. Paleoecologists have elucidated long-term changes in the biota, but the rise of environmental history (e.g., Cronon 1983, Russell 1997) and recognition that history might explain contemporary patterns emerged more recently (e.g., Foster 1992, but see also Wells et al. 1976). In areas of northeastern France deforested during the Roman occupation and farmed during 50 to 250 AD, species richness and plant communities still varied—2000 years later—with the intensity of former agriculture (Dupouey et al. 2002). In central Massachusetts, historical land use predicted forest overstory composition well in 1992, even though other major natural disturbances occurred after land use ceased (Motzkin et al. 1999). The persistent influence of land-use history in explaining the vegetation and biogeochemical characteristics of contemporary ecosystems has become increasingly apparent (Compton & Boone 2000, Foster 2002, Goodale & Aber 2001).

Natural disturbances can also leave legacies that persist for decades to centuries. For example, stand-replacing fire is the dominant disturbance in the coniferous forest landscape of Yellowstone National Park, Wyoming. Using a chronosequence approach, Kashian et al. (2005a,b) found detectable effects of historic fires on stand density and growth rate for nearly two centuries following those fires. In tropical forests of Puerto Rico, current vegetation patterns were influenced by both historical land use and hurricanes (Foster et al. 1999). Thus, the legacies of land use and disturbance can be remarkably persistent, and integrating this history with current understanding remains an important goal. We must consider the future legacies of today's landscape patterns: What variables will be most affected, and for how long? Enhanced understanding of long-term landscape development is important for both explaining the present and looking to the future.

Multiple Drivers and Their Interactions

Understanding the relative importance of different factors (and their roles at multiple scales) in producing landscape patterns is another important challenge. Most studies have focused on a dominant driver rather than on the multiple drivers that together generate spatial pattern; interactions among the varied drivers remain poorly understood, in part because they are difficult to study. Urban et al. (2002) addressed landscape patterns of vegetation in Sequoia-Kings Canyon National Park, California. These authors recognized explicitly that spatial autocorrelation in ecological data, coupled with strong patterns of correlation among environmental factors (such as the gradients governed by elevation), makes the varied agents that produce vegetation patterns difficult to disentangle.

A number of studies have related landscape patterns to variable sets that include both biophysical and socioeconomic factors or their surrogates. Interactions between land ownership and landscape position have emerged as strong determinants of land-cover patterns and changes (Mladenoff et al. 1993, Spies et al. 1994, Wear & Bolstad 1998). Black et al. (2003) assessed the role of several economic, demographic, cultural, climatic, topographic, and geologic factors in forest spatial-pattern changes (from the 1930s to the 1990s) across an 800,000-km^2 area in the interior northwest United States. Their results nicely illustrated how social-system factors are imposed on biophysical factors to generate pattern change in the study of landscape. Furthermore, the scales of response and explanatory variables often did not correspond; broad-scale factors related to land-ownership systems, economic market structures, and cultural-value systems appeared in all significant models, regardless of the response scale, and biophysical parameters related to growing conditions at the site moderated or exacerbated changes (Black et al. 2003).

Future Landscape Patterns

Forecasting future landscape patterns remains a challenging task in which the suite of drivers of landscape pattern and their interactions must be considered. The exploration of alternative scenarios and their ecological implications is particularly important in applied landscape ecology (e.g., White et al. 1997). Empirical models that use a set of independent variables to explain past land-use changes have been informative, although extrapolation of those models to the future is problematic.

A widely used approach is based on logistic regression in which the likelihood of a particular land-cover transition is estimated and simulated into the future (Wear et al. 1996, Wear & Bolstad 1998). Because the transition probabilities in these models can be influenced by many factors (e.g., elevation, distance to roads or market center, population density, and patch size), they potentially have better predictive power than simple Markov models when run in a spatial framework.

Spatially explicit simulation models are the primary tools for exploring plausible future landscape patterns and processes. For example, interactions among fire, windthrow, forest harvesting, and tree-species dynamics were explored for a 500,000-ha heterogeneous landscape of the upper Midwest United States, by use of the spatially explicit, stochastic model LANDIS (He & Mladenoff 1999). Costanza et al. (2002) developed a spatially explicit, process-based model of the 2352-km^2 Patuxent River watershed in Maryland. The model addressed the effects of both the magnitude and spatial patterns of human settlements and agricultural practices on hydrology, plant productivity, and nutrient cycling in the landscape. Such broad-scale, spatially explicit models highlight the complex nature of landscape responses. Balancing the trade-offs between the simplicity of general models and the complexity of more realistic spatial models remains a challenge.

QUANTIFYING LANDSCAPE PATTERNS

Landscape Metrics

The quantification of spatial heterogeneity is necessary to elucidate relationships between ecological processes and spatial patterns; thus, the measurement, analysis, and interpretation of spatial patterns receive much attention in landscape ecology. A wide array of metrics for landscape composition (what and how much is present, such as the number and amount of different habitat types) and configuration (how those classes are arranged spatially) were developed for categorical data. Excellent software packages are readily available; FRAGSTATS (McGarigal & Marks 1995) is used most widely. Some metrics have also been integrated into existing geographic information system (GIS) software (e.g., Patch Analyst in Arc/View). Importantly, spatial pattern analysis is a tool rather than a goal of its own, and the objectives or questions driving any analysis must be specified a priori; this specification must include the qualities of pattern to be represented and why.

A variety of issues associated with interpreting pattern metrics are now well understood by practitioners (Gustafson 1998, Haines-Young & Chopping 1996, Li & Wu 2004, Turner et al. 2001). For example, different results are obtained by analyzing different classifications of the same data (Gustafson 1998) or using different patch-definition rules. Many metrics are sensitive to changes in the grain size (spatial resolution) of the data or the extent (area) of the study landscape (e.g., Wickham & Riitters 1995), and numerous correlations occur among landscape-pattern indices (Cain et al. 1997, Riitters et al. 1995). Composition, particularly the proportions of cover types on the landscape, influences the values of many metrics (Gardner et al. 1987, Gustafson & Parker 1992, Tischendorf 2001). No single metric can adequately capture the pattern on a given landscape, and several suggestions have been made for a meaningful set of metrics that minimize redundancy while capturing the desired qualities (Riitters et al. 1995). Comparisons made among landscapes, with different data types or through time must now routinely account for these known complexities.

Despite numerous calls for improved linkages, the relationship between processes that create patterns and the patterns themselves still is not readily apparent. Krummel et al. (1987) suggested that simple, rectilinear shapes of forest patches indicated human influences in shaping landscape patterns. Numerous authors have shown that dispersed clear-cuts in forested landscapes produce distinctive landscape patterns with high patch and edge densities and small patch areas (e.g., Spies et al. 1994). The habitat loss and fragmentation associated with human land use in many regions is also well described in landscape ecology and conservation biology (e.g., Heilman et al. 2002, Riitters et al. 2000, Saunders et al. 1991). Nonetheless, no general framework exists that permits a particular spatial pattern to be linked to specific generating factors. Current research is developing a more rigorous statistical interpretation of spatial pattern analysis that rekindles the attempt to link processes with patterns and addresses several persistent challenges.

Building upon the tradition of neutral landscape models (Gardner et al. 1987, With & King 1997), Fortin et al. (2003) explored the spatial realization of simple stochastic processes on a landscape and interpreted the resulting patterns using landscape metrics. Landscape patterns were generated by independent variation of two parameters: one that represents composition (the amount of a given habitat) and one that represents configuration (its arrangement, represented here by the amount of spatial autocorrelation) of a single habitat type. Inspection of the pair-wise scatterplots between seven landscape metrics revealed that many relationships were not linear, and several were not even monotonic (Figure 1). Thus, the expectation of linear relationships among landscape metrics that has been implicit in most previous studies may be misleading.

The statistical properties and behavior of many pattern metrics remain poorly understood. Because the distributions of landscape metrics are not known, expected values and variances are not available for statistical comparisons to be made among multiple observations of a particular metric (Li & Wu 2004, Remmel & Csillag 2003, Turner et al. 2001). Remmel & Csillig (2003) used the approach of Fortin et al. (2003) to develop neutral landscape models based on composition and configuration. They generated confidence intervals for landscape metric values by collecting their empirical distribution over a series of landscapes that were simulated using values of the two parameters estimated from the observed landscape. If the confidence intervals between two landscapes overlap, then the landscapes do not differ for the given metric (Figure 2). 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. As the authors conclude, testing whether two landscape metrics differ significantly should become a standard approach.

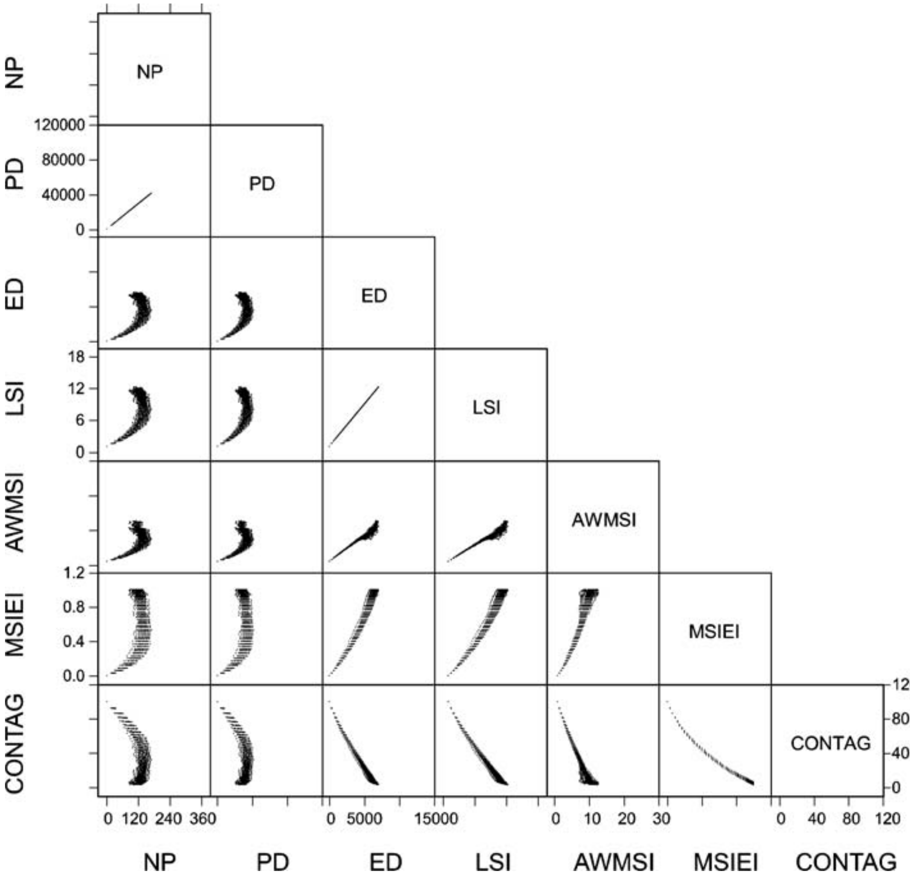

Figure 1 Scatter plots of seven landscape metrics derived from 1000 simulated binary landscapes with high autocorrelation. Abbreviations: NP, number of patches; PD, patch density; ED, edge density; LSI, landscape shape index; AWMSI, area-weighted mean shape index; MSIEI, modified Simplson's evenness index; CONTAG, contagion. The relationships are not monotonic and suggest that relationships among landscape metrics may be nonlinear. Reproduced with permission from Fortin et al. (2003).

Despite their limitations, landscape metrics remain widely used and useful. Mapped distributions of metric values (rather than the original categorical data from which they were derived) can also offer new perspectives on spatial variation across regions (Riitters et al. 2000). For example, replicate locations that share some qualities of spatial pattern are often difficult to identify; mapped distributions of metrics can be used to stratify sites for empirical study appropriately when some aspect of landscape pattern is an independent variable. Mapped patterns may also identify higher-order information not easily discernible from tabular summaries (Riitters et al. 2000).

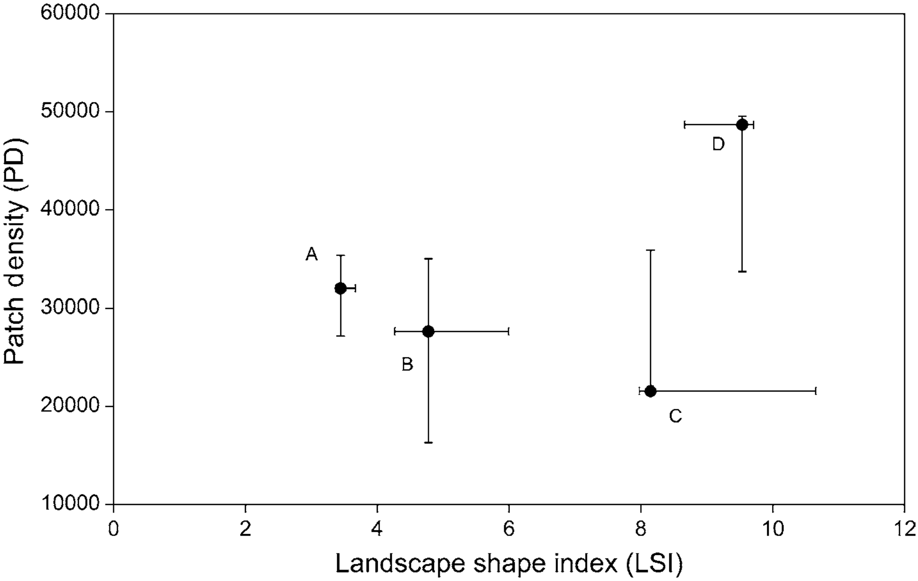

Figure 2 The 99% statistical confidence intervals for measures of patch density (PD) and landscape shape index (LSI) for four landscapes (*A–D*) near Prince George, British Columbia, Canada. *Solid circles* are actual values measured from each landscape, and confidence intervals are derived from 100 realized simulations. PD did not differ significantly among the landscapes, but LSI discriminated landscapes. Reproduced with permission from Remmel & Csillag (2003).

Spatial Statistics

Methods that treat continuous rather than discrete variation in space are receiving increased attention; the landscape metrics described above use categorical data, but spatial heterogeneity may also be continuous. Spatial statistics (Rossi et al. 1992) use the continuous distribution of a quantity of interest and do not require categorization. To illustrate the distinction, forest cover could be represented categorically (as forest or nonforest) or continuously (by tree density). Ecosystem process rates (e.g., net ecosystem production, nitrogen or carbon mineralization, and respiration) also vary continuously and, thus, may be especially amenable to analysis using spatial statistics. These methods do not depend on patch definitions or boundaries; however, additional assumptions, such as stationarity of variance in the data or isotropy, may apply.

Spatial statistics are applied somewhat less in landscape ecology than are the methods based on discrete space, but they serve several important purposes. First, the spatial structure (i.e., autocorrelation) of a variable might be quantified using spatial statistics so that sampling or data analyses can avoid locations that are spatially autocorrelated or build that structure into the study. Second, variability and the scale of spatial structure can serve as the response of interest, and spatial statistics offers efficient sampling designs to assess this (e.g., Burrows et al. 2002). However, such studies are still far from routine. Pastor et al. (1998) tested three geostatistical models of the spatial distribution of available browse, annual browse consumption, conifer basal area, and soil-nitrogen availability on Isle Royale, Michigan. Their results suggested that dynamic interactions between moose foraging and plant communities produce characteristic spatial patterns of vegetation and soil properties. For the Luquillo Experimental Forest, Puerto Rico, Wang et al. (2002) examined the spatial correlations of soil properties and environmental factors to better understand the controls on biogeochemical processes within ecosystems. They hypothesized varying degrees of spatial structure in soil organic carbon, soil moisture, and soil bulk density along gradients of elevation, slope, and aspect. Cross-correlograms indicated that soil organic carbon was correlated positively with elevation at separation distances less than 3000 m and negatively at separation distances greater than 6000 m. Fraterrigo et al. (2005) also used spatial structure as a response variable; they hypothesized and detected a change in the spatial structure of soil nutrients with historic land use. Results of such analyses may elucidate mechanisms that underpin observed patterns or suggest relationships between environmental heterogeneity and process rates of interest. Nonetheless, use of spatial statistics as responses in ecological studies still presents some challenges. For example, interpretation of semivariograms calculated for replicated spatial units is not straightforward and neither is comparison of results from different models (e.g., spherical, sinusoidal, and exponential).

Spatial statistics also offer methods for interpolating spatial patterns from point data. Kriging and cokriging, which includes environmental covariates, are used to predict values in locations where measurements have not been made. However, when Bolstad et al. (1998) compared methods for predicting vegetation patterns throughout a basin, they found that multiple regression may be stronger than cokriging if the relationships between predictor and response variables are understood.

Because the data in landscape studies are almost always spatial, spatial statistics can and should be used in conjunction with classical statistics, such as regression and analysis of variance, to determine and correct for spatial autocorrelation of errors (residuals). Statistical software packages have incorporated methods to detect and correctly model the spatial covariance structure of data, and ecological studies are beginning to implement these methods (e.g., Schwartz et al. 2003). The assumption of independent errors is important in classical statistics, and failure to account for spatial autocorrelation may lead to false conclusions (Lichstein et al. 2002).

ORGANISMS IN HETEROGENEOUS LANDSCAPES

Populations exist in spatially heterogeneous environments, and the review by Wiens (1976) may mark the beginning of a landscape approach to population dynamics. How interactions within and among populations create spatial patterns in species distributions is well developed within population ecology. For example, competition and predator-prey dynamics may produce spatial patterns in the distribution of organisms even when the underlying environment is homogeneous (Durrett & Levin 1994). How organisms create spatial patterns through spatially explicit feeding relationships and physical alterations of the environment, along with how populations respond to complex patterns and actual landscapes, is addressed in landscape ecology. Considerable overlap occurs with metapopulation biology (Hanski & Gilpin 1997) in questions and approaches.

Effects of Organisms on Landscape Heterogeneity

Although the response of organisms to landscape heterogeneity dominates research on organism-landscape interactions, the role of the biota in creating heterogeneity has also been recognized. "Ecosystem engineers" (Jones et al. 1997) are noted as key sources of heterogeneity in a variety of systems. For example, bison (*Bison bison*) drive heterogeneity patterns within the North American prairie (Knapp et al. 1999). The nightly feeding forays of hippopotami (*Hippopotamus amphibius*) create a maze of trails and canals that are movement corridors for water as well as many other species (Naiman and Rogers 1997). Despite these key examples, the role of organisms as sources of spatial heterogeneity has been somewhat understudied in landscape ecology.

Effects of Landscape Heterogeneity on Organisms

Landscape ecologists emphasize how organisms use resources that are spatially heterogeneous and how they live, reproduce, disperse, and interact in landscape mosaics. The context for much of this work has been to understand how altered landscape patterns affect the distribution, persistence, and abundance of species, often in the face of land management controversies [e.g., Northern Spotted Owls (*Strix occidentalis caurina*) (Murphy & Noon 1992)]. Effects of habitat loss and fragmentation have received much attention (e.g., Andrén 1994, Fahrig 2003, Haila 2002, Saunders et al. 1991).

Much has been learned from studies that have evaluated factors that explain variation in the presence or abundance or organisms in the landscape. Patch size has a strong effect on edge and interior species but is negligible for generalist species (Bender et al. 1998). However, local habitat conditions may be inadequate to explain species presence or abundance; a significant effect of boundary shape or characteristics of the surrounding landscape—usually referred to as landscape context (Mazerolle & Villard 1999)—may be present. For example, empirical studies of butterfly taxa in landscapes with naturally isolated meadows demonstrated that the matrix that surrounds patches could influence their effective isolation (Ricketts 2001). In an experiment that controlled for patch area, Tewksbury et al. (2002) found that pollination and seed dispersal, two key plant–animal interactions, were facilitated by the presence of corridors that connect habitat patches. Murphy & Lovett-Doust (2004) argue for an integration of metapopulation and landscape-ecological approaches for understanding regional dynamics in plants, emphasizing notions of connectivity and context to describe components of variability in the landscape from a species-specific perspective.

Analyses conducted at multiple scales have demonstrated the importance of landscape context for a wide range of taxa (e.g., Lindenmayer et al. 1999, Pearson et al. 1995, Steffan-Dewenter et al. 2002, Stoner & Joern 2004), although the influence may be less if the focal habitat is abundant and well connected (e.g., Miller et al. 2004a). Many studies have also demonstrated that habitat connectivity is scale dependent; that is, whether a given pattern of habitat is connected depends on the mobility of the species and the pattern of the habitat (Goodwin & Fahrig 2002, Vos et al. 2001). Organisms may respond to multivariate habitat heterogeneity at multiple scales, and identification of the factors and scales that best explain variation in the presence or abundance of organisms remains a key goal in landscape ecology.

Disentangling the effects of landscape composition (what and how much is there) and landscape configuration (how is it spatially arranged) on populations is an important area of current research (Fahrig 1997, McGarigal & Cushman 2002). In their review of 134 published fragmentation studies, McGarigal & Cushman (2002) concluded that the ecological mechanisms and effects of habitat fragmentation on populations remain poorly understood. Evidence is mounting for a primary effect of composition and secondary effect of configuration. Field studies of forest-breeding birds conducted in 94 landscapes of 10 × 10 km each found a consistent positive relationship between forest cover and the distribution of forest-breeding birds but weaker and variable effects of forest fragmentation (Trzcinski et al. 1999). In a study of the incidence of herbaceous species in deciduous forests of south Sweden, Dupré & Ehrlén (2002) found that habitat quality was more important than habitat configuration. Moreover, the importance of habitat configuration varied with life history; species that were habitat specialists and clonal perennials that produced fewer seeds were more likely to be affected negatively by patch isolation. Animal-dispersed species were more negatively affected by small stand size than were species dispersed by other mechanisms (Dupré & Ehrlén 2002).

Simulation studies also suggest that changes in landscape composition are likely to have a greater effect on population persistence than are changes in landscape configuration. Fahrig & Nuttle (2005) hypothesize that landscape configuration will be important only if configuration has a large effect on among-patch movements and among-patch movements have a large effect on population survival. Results of a modeling study by Flather & Bevers (2002) found that, over a broad range of habitat amounts and arrangements, population size was largely determined by the abundance of habitat. However, habitat configuration became important in landscapes with low habitat abundance, in which dispersal mortality became important. King & With (2002) obtained similar results in which spatial pattern was important for poorly dispersed species that occurred in landscapes with low habitat abundance.

Landscape ecology has also focused attention on developing more sophisticated habitat assessments for the distribution of biota. One approach maintains the simple categorization of suitable versus unsuitable habitat but reassesses the landscape for different taxa using rules and scales appropriate for each species or functional group (e.g., Addicott et al. 1987, Pearson et al. 1999). Knight & Morris (1996) used evolutionary theories to document how density-dependent habitat selection and habitat variation could be applied to identify habitats in landscapes. Statistical methods such as resource-selection functions (Manly et al. 2002) that are based on logistic regression provide multivariate and continuous assessments of habitat selection by different taxa that can be evaluated across a range of scales. These analyses employ a used versus available design and are frequently conducted across multiple scales (e.g., Boyce et al. 2003). Studies of this sort clearly demonstrate that the same landscape may look very different to different species and underscore the importance of an organism-centered view of landscape heterogeneity (Wiens 1989).

Recent studies identify important situations in which the patch-based framework simply does not apply and suggest the need for a broader conceptual framework of spatial pattern. For example, the dendritic metapopulations that characterize fish and other species constrained to disperse within river-creek systems are not well represented by either a linear or a two-dimensional representation of spatial structure and metapopulation dynamics (Fagan 2002). Fagan (2002) combined a simple geometric model with a metapopulation model and empirical data to explore the consequences of dendritic landscapes. Depending on dispersal details, the connectivity patterns of dendritic landscapes could either enhance or reduce metapopulation persistence compared with linear systems. Furthermore, the specific location of fragmentation events becomes especially important in the dendritic systems.

A recent call for the integration of landscape ecology and population genetics (Manel et al. 2003) suggests opportunities for new insights about how geographical and environmental features structure genetic variation and for reconstruction of the spatial movements and spread of populations. In particular, landscape genetics may yield new insights regarding the spread of invasive species and native species, such as top predators, that are recovering from earlier extirpation and dispersing in heterogeneous landscapes (Lucchini et al. 2002, Reuness et al. 2003) or responding to landscape change (e.g., Keyghobadi et al. 1999).

The spatial implications of trophic cascades suggest important effects of spatial heterogeneity on species interactions. 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 increased seed predation (Tallmon et al. 2003). In a sophisticated study of predator-prey dynamics, With et al. (2002) determined how landscape structure affected the ability of two species of ladybird beetle (Coleoptera: Coccinellidae) to track aphid populations in experimental landscapes that differed in the abundance and fragmentation of red clover (*Trifolium pratense*). A compelling finding from this study was that thresholds in landscape structure can be perpetuated across trophic levels, producing similar thresholds in the distribution of pest populations and suggesting a mechanistic link between individual movements and population-level phenomena that affect predator-prey interactions in fragmented landscapes. The effects of predator-herbivore-plant relationships on spatial variability in plant communities is also intriguing. Top predators may influence their herbivore prey populations numerically, by reducing population size, or behaviorally, by influencing patterns of habitat use. When spatially variable, these top-down effects may ultimately influence the landscape vegetation patterns (Schmitz et al. 2000).

More broadly, need exists for addressing community dynamics in heterogeneous landscapes. Opdam et al. (2003) noted that a major gap in studies of population persistence in heterogeneous landscapes is the lack of methods to transfer studies on single species to generalized knowledge about the relation between landscape pattern and biodiversity. Most studies have indeed focused on single species, or perhaps functional groups, yet understanding species assemblages, especially in changing landscapes, bears further study.

LANDSCAPE HETEROGENEITY AND DISTURBANCE

Studies of disturbance and succession continue to generate new understanding about the interactions between ecological processes and landscape pattern. A disturbance is “any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment” (Pickett & White 1985). Disturbances often result in “open space” and, through their gradients of severity, introduce complex spatial heterogeneity. Furthermore, the occurrence or effects of disturbance may depend on the system’s state before the disturbance occurred. Thus, disturbances are particularly interesting in landscape ecology because they both respond to and create spatial heterogeneity at multiple scales.

Enhanced understanding of landscape disturbance dynamics underlies the important conceptual shift that recognized dynamic equilibria and nonequilibrium systems in ecology (Perry 2002, Turner et al. 1993, Wu & Loucks 1995). Indeed, Wu & Loucks (1995) argued that the past inability to incorporate heterogeneity and multiple scales into quantitative expressions of stability led, in part, to the failure of the classical equilibrium paradigm in ecology. From a nonequilibrium perspective, stochastic events such as disturbance alter system state and trajectory and are integral to the system. Equilibrium is but one of several outcomes, and it may be apparent only at certain scales (Turner et al. 1993). Empirical studies of several landscapes found marked fluctuations in landscape composition (e.g., Baker 1989), particularly when disturbances were large and infrequent (Moritz 1997, Turner et al. 1993). The steady-state mosaic, in which sites are in different stages of succession but the landscape proportions of successional stages remain constant, was found to apply only in some cases.

Effects of Disturbance on Landscape Heterogeneity

Disturbances produce a mosaic of disturbed versus undisturbed areas and complex spatial variation in severities within disturbed areas. Foster et al. (1998) used several examples from large, infrequent disturbances to illustrate the diverse spatial patterns that can result. Single-disturbance types have been reasonably well studied, but less is known about interacting disturbances or whole disturbance regimes; this feature is an important thrust of current research. Paine et al. (1998) suggested that particular co-occurrences or sequences of different disturbances could produce ecological surprises or qualitative shifts in the system state. For example, the composition of the southern boreal forest changed substantially in a century in response to climate-driven changes in fire frequency, forest fragmentation, and logging. They suggest that understanding the ecological synergisms among disturbances is basic to future environmental management (Paine et al. 1998).

Studies designed to understand the combined contingent effects of multiple disturbances are promising. Interactions between fire and spruce-beetle (*Dendroctonus ruÞpennis*) outbreaks over more than a century were studied in a 2800-km^2 landscape by Bebi et al. (2003). Results showed that fire history had the greatest effect on stand susceptibility to spruce-beetle outbreak. Radeloff et al. (2000) also found that interactions between disturbances, here jack pine–budworm defoliation and salvage logging, substantially changed landscape heterogeneity in the pine barrens of northwest Wisconsin, and they hypothesized that the presettlement landscape patterns were shaped by interactions between insect defoliators and fire.

Changing disturbance regimes is another important area of current research. Because disturbances are such important agents of pattern formation in landscapes, changes in their frequency, intensity, or extent may well alter landscape structure. However, how much do disturbance regimes need to shift before landscape patterns are altered qualitatively? The answer is not known, yet it assumes increasing importance in the context of global change. Many disturbances, such as fires, floods, and hurricanes, have a strong climate forcing, and development pressure is increasing in many disturbance-prone sites (e.g., Hansen et al. 2002). How altered landscapes will themselves influence disturbance regimes is not known.

Landscape management often relies, either implicitly or explicitly, on an understanding of disturbance regimes. Management may attempt to mimic spatial and temporal patterns of disturbance or seek to maintain or return a landscape to its historic range of variability (HRV) (Landres et al. 1999). Considerable discussion has occurred about the use of the timing and spatial patterns of natural disturbances as a model for human activities (e.g., Attiwill 1994). This approach implicitly assumes that ecological processes will be better maintained in this way, and current management of the Ontario Crown Lands, Canda, offers an excellent example of implementing these concepts at a broad scale (Perera et al. 2000).

Effect of Landscape Heterogeneity on Disturbance

Assessment of the role of landscape heterogeneity on the spread of disturbance was identified at an early workshop as one of the key questions in landscape ecology (Risser et al. 1984) and was the theme of the first U.S. landscape ecology symposium. A number of studies have now documented significant influences of landscape heterogeneity on the spread or effects of disturbances. Effects of hurricanes, wind events, and fires can vary with spatial location on the landscape; researchers have frequently found a strong influence of landform on these effects. For example, the severity of hurricanes on vegetation varies with the exposure of the sites (Boose et al. 1994). In vast, relatively unlogged forests of coastal Alaska, Kramer et al. (2001) documented a spatially predictable windthrow gradient that contrasted sharply with the prior emphasis on gap-phase disturbances in these forests. In the southern Appalachian Mountains, changes in land use and land cover are often concentrated at the low to mid elevation, sheltered positions near streams that coincide with species-rich cove hardwood forests (Turner et al. 2003, Wear & Bolstad 1998). Thus, landscape position can influence susceptibility to disturbance and, hence, the spatial heterogeneity of disturbance severity.

Jules et al. (2002) investigated the role of heterogeneity in governing the spread of an invasive disease (a fatal root pathogen, *Phytophthora lateralis*) on a patchily distributed conifer, Port Orford cedar (*Chamaecyparis lawsoniana*). Their study showed that cedar populations along creeks crossed by roads were more likely to be infected than were those on creeks without road crossings; furthermore, the pathogen spread farther if it was vectored along roads. Studies have shown a strong influence of patch size and juxtaposition on incidence of Lyme disease by alteration of the community composition of vertebrate hosts and the abundance of larval ticks (*Ixodes scapularis*) (Allan et al. 2003). Indeed, the integration of landscape ecology and epidemiology may offer new approaches for understanding emerging infectious diseases and the effects of global change on vector-borne diseases (Kitron 1998).

In general, landscape position influences disturbance when the disturbance has a distinct directionality or locational specificity such that some locations are exposed more than others. However, the disturbance also must be of moderate intensity such that it can respond to gradients in the landscape—for example, fires burning under extreme conditions may show little variation in effects with landscape position (Moritz 1997). Accordingly, no predictable effect of landscape position is seen when the disturbance has no directionality, such as the smaller gap-forming downbursts in the upper midwestern United States (Frelich & Lorimer 1991) or when intensity is extremely high (Moritz 1997).

ECOSYSTEM PROCESSES IN HETEROGENEOUS LANDSCAPES

The interface of ecosystem and landscape ecology is less developed than are the previous research areas, despite a tradition in Eastern Europe (e.g., Ryszkowski et al. 1999) and stronger connections during the early development of landscape ecology in North America. Ecosystem ecology has largely considered fluxes of matter and energy in the absence of a spatial context, and landscape ecology has had less focus on ecosystem processes. 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, which represent losses from donor ecosystems and subsidies to recipient ecosystems, for the long-term sustainability of ecosystems is also now acknowledged (Chapin et al. 2002, Reiners & Driese 2004). The patterns, causes, and consequences of spatial heterogeneity for ecosystem function are recognized as a current research frontier in both landscape ecology and ecosystem ecology (Lovett et al. 2005).

Progress has been made in the effort to recognize and explain spatial heterogeneity in ecosystem process rates that are either measured or simulated at many points. The role of landscape position has been elucidated (Soranno et al. 1999), and regional variation in a variety of stocks and processes (soil organic matter or carbon, denitrification, and net nitrogen mineralization rates) has been explored (e.g., Burke et al. 2002, Groffman et al. 1992). For example, the relationship between soil nitrogen mineralization and both biotic and abiotic factors was analyzed and mapped for the midwestern Great Lakes region of the United States (Fan et al. 1998). In the Greater Yellowstone Ecosystem, spatial patterns of aboveground net primary production were predicted by elevation and cover type (Hansen et al. 2000).

Broad conceptual frameworks have considered the conditions under which spatial pattern, or particular aspects of spatial pattern, should influence a lateral flux. Wiens et al. (1985) proposed a framework for lateral fluxes that included the factors that determine boundary locations, how boundaries affect 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 that move from a source ecosystem to an aquatic system. Loreau et al. (2003) developed a metaecosystem framework by extending metapopulation models to represent fluxes of matter or energy. Simulation models ranging from simple representations (e.g., Gardner et al. 1992) to complex, process-based spatial models (e.g., Costanza et al. 2002) have also been employed to identify the aspects of spatial configuration that could enhance or retard a lateral flux. Strayer et al. (2003b) 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 semiarid systems (e.g., Tongway & 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 (Strayer et al. 2003a). Most of these studies focus on nutrients, such as nitrogen or phosphorus, related to surface water quality (e.g., Jordan et al. 1997, Soranno et al. 1996). 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. For example, landscape heterogeneity explained from 65% to 86% of the variation in nitrogen yields to streams in the U.S. Mid-Atlantic region (Jones et al. 2001). 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.

CONCLUSIONS AND FUTURE DIRECTIONS

Landscape ecology is now well integrated with the ecological sciences. Consideration of spatial heterogeneity, which requires a conscious decision about whether and how to include it, has become the norm. Reasonable consensus about the approaches for quantifying landscape structure exists, but general relationships between generative processes and resulting patterns remain elusive. However, there is now an extensive library of empirical studies that explore ecological responses to landscape patterns. The multiple approaches suggested at the close of my 1989 article have in fact been widely applied in landscape studies.

Applications represent an important test of new conceptual frameworks and knowledge, and the demand for applied landscape ecology remains high (Liu & Taylor 2002). Networks of conservation areas based on the understanding of multispecies responses to landscape mosaics are providing a basis for long-term landscape planning in Europe (e.g., Bruinderink et al. 2003). In Ontario, Canada, legislation mandating that Crown forests be managed to keep landscape patterns consistent with long-term norms emerged directly from new understanding of landscape heterogeneity and disturbance (Perera et al. 2000). Forest-harvest strategies now incorporate consideration of the spatial landscape dynamics and the effects on a variety of species (Boutin & Herbert 2002). Predictions of invasive species (With 2002) and water quality (Strayer et al. 2003a) require consideration of landscape patterns.

Spatial extrapolation offers another mechanism for rigorous testing of the relationships between spatial patterns and processes (Miller et al. 2004b). Whether based on empirical observation or simulation modeling, the prediction of pattern (and the associated uncertainties) followed by testing with independent data or through cross validation offers a powerful way to evaluate current understanding. Understanding of the causes and effects of spatial heterogeneity will be enhanced by closely examining the conditions under which spatial extrapolation fails or succeeds (Miller et al. 2004b). Scaling remains challenging, despite numerous calls for progress during the past 15 years. However, scaling rules that integrate the scale dependency of patterns and processes in ways that organisms scale their responses to these patterns and processes are promising (Ludwig et al. 2000).

Where are the key directions for future research in landscape ecology? Interaction is a key theme related to several current research areas: interactions among multiple drivers that generate spatial patterns, particularly biophysical and socioeconomic factors; interactions among different kinds and scales of disturbances; and interactions among trophic levels in landscape mosaics. Landscape ecology should lead the next generation of studies taking a more comprehensive look at ecological dynamics in heterogeneous landscapes. A compelling need for expanding the temporal horizon of landscape studies also exists. Paleoecological studies provide critical context for understanding landscape dynamics, and historical dynamics shape current landscapes and may constrain future responses. Contemporary land-use patterns are creating future legacies, yet these potential legacies remain poorly understood.

Enhanced understanding of the ecological importance of spatial nonlinearities and thresholds remains an important research challenge. If important nonlinearities or thresholds are present among interacting variables, then landscape patterns may be even more difficult to predict, and unexpected changes in the state of an ecosystem or landscape may ensue (Frelich & Reich 1999, Groffman et al. 2005). Critical thresholds in spatial pattern have been suggested from theoretical and empirical studies, but a prediction of when a system is nearing a threshold is still difficult to make (Groffman et al. 2005).

Much remains to be learned about ecosystem processes in heterogeneous landscapes. 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. A landscape perspective still offers a prime opportunity for linking populations and ecosystem processes and services (Lundberg & Moberg 2003); organisms exist in heterogeneous space, and they use, transform, and transport matter and energy. Augustine & Frank (2001) demonstrated an influence of grazers on the distribution of soil nitrogen properties 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. Herbivore-mediated changes in forest composition have been shown to have important implications for patterns of nutrient cycling (Pastor et al. 1998, 1999). Studies have also identified the role of piscivores in the transportation of nutrients derived from aquatic ecosystems to terrestrial ecosystems through their foraging patterns (e.g., 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 enhance functional understanding of landscape mosaics.

In conclusion, landscape ecology has matured. As noted by Wiens (1999), the discipline draws strength from the distinctiveness of its approach—its emphasis on spatial patterns and relationships, scaling, heterogeneity, boundaries, and flows of energy and materials in space. 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 a more mechanistic understanding of the reciprocal relationships between pattern and process.

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LITERATURE CITED

Addicott JF, Aho JM, Antolin MF, Padilla DK, Richardson JS, Soluk DA. 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos* 49:340–46

Allan BF, Keesing F, Ostfeld RS. 2003. Effect of forest fragmentation on Lyme disease risk. *Conserv. Biol.* 17:267–72

Andrén H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat. *Oikos* 71:355–66

Attiwill PM. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. *Forest Ecol. Manag.* 63:247–300

Augustine DJ, Frank DA. 2001. Effects of migratory grazers on spatial heterogeneity of soil nitrogen properties in a grassland ecosystem. *Ecology* 82:3149–62

Baker WL. 1989. Landscape ecology and nature reserve design in the Boundary Waters Canoe Area, Minnesota. *Ecology* 70:23–35

Bastian O. 2001. Landscape ecology: towards a unified discipline? *Landsc. Ecol.* 16:757–66

Bebi P, Kulakowski D, Veblen TT. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. *Ecology* 84:362–71

Bell SS, Robbins BD, Jensen SL. 1999. Gap dynamics in a seagrass landscape. *Ecosystems* 2:493–504

Bender DJ, Contreras TA, Fahrig L. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* 79: 517–33

Black AE, Morgan P, Hessburg PF. 2003. Social and biophysical correlates of change in forest landscapes of the interior Columbia Basin, USA. *Ecol. Appl.* 13:51–67

Bolstad PV, Swank W, Vose J. 1998. Predicting Southern Appalachian overstory vegetation with digital terrain data. *Landsc. Ecol.* 13:271–83

Boose ER, Foster DR, Fluet M. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecol. Monogr.* 64:369–400

Boutin S, Hebert D. 2002. Landscape ecology and forest management: developing an effective partnership. *Ecol. Appl.* 12:390–97

Boyce MS, Mao JS, Merrill EH, Fortin D, Turner MG, et al. 2003. Scale and heterogeneity in habitat selection by elk in

Yellowstone National Park. *EcoScience* 10:421–31

Bruinderink GG, Van Der SluisT, Lammertsma D, Opdam P, Pouwels R. 2003. Designing a coherent ecological network for large mammals in northwestern Europe. *Conserv. Biol.* 17:549–57

Burke IC, Lauenroth WK, Cunfer G, Barrett JE, Mosier A, et al. 2002. Nitrogen in the central grasslands region of the United States. *BioScience* 52:813–23

Burrows SN, Gower ST, Clayton MK, Mackay DS, Ahl DE, et al. 2002. Application of geostatistics to characterize leaf area index (LAI) from flux tower to landscape scales using a cyclic sampling design. *Ecosystems* 5:667–79

Cain DH, Riitters K, Orvis K. 1997. A multiscale analysis of landscape statistics. *Landscape Ecol.* 12:199–212

Chapin FS III, Matson PA, Mooney HA. 2002. *Principles of Terrestrial Ecosystem Ecology*. New York: Springer-Verlag. 436 pp.

Compton JE, Boone RD. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. *Ecology* 81: 2314–30

Costanza R, Voinov A, Boumans R, Maxwell T, Villa F, et al. 2002. Integrated ecological economic modeling of the Patuxent River watershed, Maryland. *Ecol. Monogr.* 72:203–32

Cronon W. 1983. *Changes in the Land: Indians, Colonists and the History of New England.* New York: Hill & Wang. 241 pp.

Dupouey JL, Dambrine E, Laffite JD, Moares C. 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology* 83:2978–84

Dupré C, Ehrlén J. 2002. Habitat configuration, species trains and plant distributions. *J. Ecol.* 90:796–805

Durrett R, Levin SA. 1994. Stochastic spatial models: a user's guide to ecological applications. *Philos. Trans. R. Soc. London Ser. B.* 343:329–50

Fagan WF. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology* 83:3243–49

Fahrig L. 1997. Relative effects of habitat loss and fragmentation on population extinction. *J. Wildl. Manag.* 61:603–10

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 34:487–15

Fahrig L, Nuttle WK. 2005. Population ecology in spatially heterogeneous environments. In *Ecosystem Function in Heterogeneous Landscapes*, ed. GM Lovett, CG Jones, MG Turner, KC Weathers. New York: Springer-Verlag. In press

Fan W, Randolph JC, Ehman JL. 1998. Regional estimation of nitrogen mineralization in forest ecosystems using Geographic Information Systems. *Ecol. Appl.* 8:734–47

Flather CH, Bevers M. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *Am. Nat.* 159:40–56

Fortin M-J, Boots B, Csillag F, Remmel TK. 2003. On the role of spatial stochastic models in understanding landscape indices. *Oikos* 102:203–12

Foster DR. 1992. Land-use history (1730–1990) and vegetation dynamics in central New England, USA. *J. Ecol.* 80:753–72

Foster DR. 2002. Insights from historical geography to ecology and conservation: lessons from the New England landscape. *J. Biogeogr.* 29:1269–75

Foster DR, Fluet M, Boose ER. 1999. Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecol. Appl.* 9:555–72

Foster DR, Knight DH, Franklin JF. 1998. Landscape patterns and legacies resulting from large infrequent forest disturbances. *Ecosystems* 1:497–510

Fraterrigo J, Turner MG, Pearson SM, Dixon P. 2005. Effects of past land use on spatial heterogeneity of soil nutrients in Southern Appalachian forests. *Ecol. Monogr.* 75:215–30

Frelich LE, Lorimer CG. 1991. Natural disturbance regimes in hemlock-hardwood forests of the upper Great Lakes region. *Ecol. Monogr.* 61:145–64

Frelich LE, Reich PB. 1999. Neighborhood effects, disturbance severity, and community stability in forests. *Ecosystems* 2:151–66

Gardner RH, Milne BT, Turner MG, O'Neill RV. 1987. Neutral models for the analysis of broad-scale landscape patterns. *Landsc. Ecol.* 1:19–28

Gardner RH, Dale VH, O'Neill RV, Turner MG. 1992. A percolation model of ecological flows. In *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flow*, ed. AJ Hansen, F Di Castri, 259–69. New York: Springer-Verlag

Gergel SE, Turner MG, Miller JR, Melack JM, Stanley EH. 2002. Landscape indicators of human impacts to river-floodplain systems. *Aquat. Sci.* 64:118–28

Goodale CL, Aber JD. 2001. The long-term effects of land-use history on nitrogen cycling in northern hardwood forests. *Ecol. Appl.* 11:253–67

Goodwin BJ, Fahrig L. 2002. How does landscape structure influence landscape connectivity? *Oikos* 99:552–70

Groffman PM, Baron JS, Blett T, Gold AJ, Goodman I, et al. 2005. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? *Ecosystems*. In press

Groffman PM, Tiedje TM, Mokma DL, Simkins S. 1992. Regional-scale analysis of denitrification in north temperate forest soils. *Landsc. Ecol.* 7:45–54

Gustafson EJ. 1998. Quantifying landscape spatial pattern: What is the state of the art? *Ecosystems* 1:143–56

Gustafson EJ, Parker GR. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. *Landsc. Ecol.* 7:101–10

Haila Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecol. Appl.* 12: 321–34

Haines-Young R, Chopping M. 1996. Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. *Prog. Phys. Geog.* 20:418–45

Hansen AJ, Rotella JJ, Kraska MPV, Brown D. 2000. Spatial patterns of primary productivity in the greater Yellowstone ecosystem. *Landsc. Ecol.* 15:505–22

Hansen AJ, Rasker R, Maxwell B, Rotella JJ, Johnson JD, et al. 2002. Ecological causes and consequences of demographic change in the new west. *BioScience* 5:151–62

Hanski IA, Gilpin ME, eds. 1997. *Metapopulation Biology*. New York, NY: Academic. 512 pp.

Hargis CD, Bissonette JA, David JL. 1998. The behavior of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecol.* 13:167–86

He HS, Mladenoff DJ. 1999. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. *Ecology* 80:81–99

Heilman GE, Strittholt JR, Slosser NC, Dellasala DA. 2002. Forest fragmentation of the conterminous United States: assessing forest intactness through road density and spatial characteristics. *BioScience* 52:411–22

Jones CG, Lawton JH, Shachak M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946–57

Jones KB, Neale AC, Nash MS, Van Remortel RD, Wickham JD, et al. 2001. Predicting nutrient and sediment loadings to streams from landscape metrics: a multiple watershed study from the United States mid-Atlantic region. *Landscape Ecol.* 16:301–12

Jordan TE, Correll DL, Weller DE. 1997. Relating nutrient discharges from watersheds to land use and streamflow variability. *Water Resour. Res.* 33:2579–90

Jules ES, Kauffman MJ, Ritts WD, Carroll AL. 2002. Spread of an invasive pathogen over a variable landscape: a nonnative root rot on Port Orford cedar. *Ecology* 83:3167–81

Kashian DM, Turner MG, Romme WH. 2005a. Changes in leaf area and stemwood increment with stand development in Yellowstone National Park: relationships between forest stand structure and function. *Ecosystems*. 8:48–61

Kashian DM, Turner MG, Romme WH, Lorimer CJ. 2005b. Variability and convergence in stand structure with forest development on a fire-dominated landscape. *Ecology.* 86:643–54

Keyghobadi N, Roland J, Strobeck C. 1999. Influence of landscape on the population genetic structure of the alpine butterfly *Parnassius smintheus* (Papilionidae). *Mol. Ecol.* 8:1481–95

King AW, With KA. 2002. Dispersal success on spatially structured landscapes: When do spatial pattern and dispersal behavior really matter? *Ecol. Model.* 147:23–39

Kitron U. 1998. Landscape ecology and epidemiology of vector-borne diseases: tools for spatial analysis. *J. Med. Entomol.* 35:435–45

Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, et al. 1999. The keystone role of bison in North American tallgrass prairie—Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience* 49:39–50

Knight TW, Morris DW. 1996. How many habitats do landscapes contain? *Ecology* 77: 1756–64

Kramer MG, Hansen AJ, Taper ML, Kissinger EJ. 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. *Ecology* 82:2749–68

Krummel JR, Gardner RH, Sugihara G, O'Neill RV, Coleman PR. 1987. Landscape patterns in a disturbed environment. *Oikos* 48:321–24

Landres PB, Morgan P, Swanson FJ. 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.* 9:1179–88

Levin SA. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–83

Li H, Reynolds JF. 1995. On definition and quantification of heterogeneity. *Oikos* 73: 280–84

Li HB, Wu JG. 2004. Use and misuse of landscape indices. *Landsc. Ecol.* 19:389–99

Lichstein JW, Simons TR, Shriner SA, Franzreb KE. 2002. Spatial autocorrelation and autoregressive models in ecology. *Ecol. Monogr.* 72:445–63

Lindenmayer DB, Cunningham RB, Pope ML, Donnelly CF. 1999. The response of arboreal marsupials to landscape context: a large-scale fragmentation study. *Ecol. Appl.* 9: 594–611

Liu J, Taylor WW, eds. 2002. *Integrating Landscape Ecology into Natural Resource Management*. Cambridge, UK: Cambridge Univ. Press. 480 pp.

Loreau M, Mouquet N, Holt RD. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecol. Lett.* 6:673–79

Lovett GM, Jones CG, Turner MG, Weathers KC, eds. 2005. Ecosystem function in heterogeneous landscapes. New York: Springer-Verlag. In press

Lucchini V, Fabbri E, Marucco F, Ricci S, Boitani L, et al. 2002. Noninvasive molecular tracking of colonizing wolf (*Canis lupus*) packs in the western Italian Alps. *Mol. Ecol.* 11:857–68

Ludwig JA, Wiens JA, Tongway DJ.2000.A scaling rule for landscape patches and how it applies to conserving soil resources in savannas. *Ecosystems* 3:84–97

Lundberg J, Moberg F. 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. *Ecosystems* 6:87–98

Manel S, Schwartz MK, Luikart G, Taberlet P. 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends Ecol. Evol.* 18:189–97

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002. *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Dordrect, The Netherlands: Kluwer Acad. 221 pp.

Mazerolle MJ, Villard MA. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. *Ecoscience* 6:117–24

McGarigal K, Cushman SA. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecol. Appl.* 12:335–45

McGarigal K, Marks BJ. 1995. FRAGSTATS. Spatial analysis program for quantifying landscape structure. *USDA For. Serv. Gen. Tech. Rep.* PNW-GTR-351

Miller JR, Dixon MD, Turner MG. 2004a. Response of avian communities in large-river floodplains to environmental variation at multiple scales. *Ecol. Appl.* 14:1394–10

Miller JR, Turner MG, Smithwick EAH, Dent CL, Stanley EH. 2004b. Spatial extrapolation: the science of predicting ecological patterns and processes. *BioScience* 54:310–20

Mladenoff DJ, White MA, Pastor J, Crow TR. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. *Ecol. Appl.* 3:294–306

Moritz MA. 1997. Analyzing extreme disturbance events: fire in Los Padres National Forest. *Ecol. Appl.* 7:1252–62

Motzkin G, Wilson GP, Foster DR, Arthur A. 1999. Vegetation patterns in heterogeneous landscapes: the importance of history and environment. *J. Veg. Sci.* 10:903–20

Murphy HT, Lovett-Doust J. 2004. Context and connectivity in plant metapopulations and landscape mosaics: Does the matrix matter? *Oikos* 105:3–14

Murphy DD, Noon BR. 1992. Integrating scientific methods with habitat conservation planning—reserve design for northern spotted owls. *Ecol. Appl.* 2:3–17

Naiman RJ, Rogers KH. 1997. Large animals and system level characteristics in river corridors. *BioScience* 47:521–29

Naiman RJ, Bilby RE, Schindler DE, Helfield JM. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5:399–17

Opdam P, Foppen R, Vos C. 2002. Bridging the gap between ecology and spatial planning in landscape ecology. *Landsc. Ecol.* 16:767–79

Opdam P, Verboom J, Pouwels R. 2003. Landscape cohesion: an index for the conservation potential of landscapes for biodiversity. *Landsc. Ecol.* 18:113–26

Paine RT, Tegner MJ, Johnson EA. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1:535–45

Palmer MA, Swan CM, Nelson K, Silver P, Alvestad R. 2000. Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. *Landsc. Ecol.* 15:563–76

Parker KC, Bendix J. 1996. Landscape-scale geomorphic influences on vegetation patterns in four environments. *Phys. Geogr.* 17: 113–41

Pastor J, Dewey B, Moen R, Mladenoff DJ, White M, et al. 1998. Spatial patterns in the moose-forest-soil ecosystem on Isle Royale, Michigan, USA. *Ecol. Appl.* 8:411–24

Pastor J, Cohen Y, Moen R. 1999. Generation of spatial patterns in boreal forest landscapes. *Ecosystems* 2:439–50

Pearson SM, Turner MG, Drake JB. 1999. Landscape change and habitat availability in the southern Appalachian highlands and the Olympic Peninsula. *Ecol. Appl.* 9:1288–04

Pearson SM, Turner MG, Wallace LL, Romme WH. 1995. Winter habitat use by large ungulates following fires in northern Yellowstone National Park. *Ecol. Appl.* 5:744–55

Perera AH, Euler DL, Thompson ID, eds. 2000. *Ecology of a Managed Terrestrial Landscape: Patterns and Processes of Forest Landscapes in Ontario.* Vancouver, BC: UBC Press. 336 pp.

Perry GLW. 2002. Landscapes, space and equilibrium: shifting viewpoints. *Prog. Phys. Geog.* 26:339–59

Pickett STA, Cadenasso ML. 1995. Landscape ecology: spatial heterogeneity in ecological systems. *Science* 269:331–34

Pickett STA, White PS, eds. 1985. *The Ecology of Natural Disturbance and Patch Dynamics.* New York: Academic. 472 pp.

Radeloff VC, Mladenoff DJ, Boyce MS. 2000. Effects of interacting disturbances on landscape patterns: budworm defoliation and salvage logging. *Ecol. Appl.* 10:233–47

Reiners WA, Driese KL. 2004. *Transport Processes in Nature*. Cambridge,UK: Cambridge Univ. Press. 302 pp.

Reuness EK, Stenseth NC, O'Donoghue M,

Boutin S, Ellegren H, et al. 2003. Ecological and genetic sptial structuring in the Canada lynx. *Nature* 425:69–72

Remmel TK, Csillag F. 2003. When are two landscape pattern indices significantly different? *J. Geogr. Syst.* 5:331–51

Ricketts TH. 2001. The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* 158:87–99

Riitters K, Wickham J, O'Neill R, Jones B, Smith E. 2000. Global-scale patterns of forest fragmentation. *Conserv. Ecol.* 4(2):3. http://www.consecol.org/vol4/iss2/art3/

Riitters KH, Wickham JD, O'Neill RV, Jones KB, Smith ER, et al. 2002. Fragmentation of continental United States forests. *Ecosystems* 5:815–22

Riitters KH, O'Neill RV, Hunsaker CT, Wickham JD, Yankee DH, et al. 1995. A factor analysis of landscape pattern and structure metrics. *Landsc. Ecol.* 10:23–40

Risser PG, Karr JR, Forman RTT. 1984. Landscape ecology: directions and approaches. *Spec. Publ. No.2*, Ill. Nat. Hist. Surv., Champaign, Ill.

Rossi RE, Mulla DJ, Journel AG, Franz EH. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecol. Monogr.* 62:277–314

Russell EB. 1997. *People and the Land Through Time*. New Haven: Yale Univ. Press. 306 pp.

Ryszkowski L, Bartoszewicz A, Kedziora A. 1999. Management of matter fluxes by biogeochemical barriers at the agricultural landscape level. *Landsc. Ecol.* 14:479–92

Saunders D, Hobbs RJ, Margules CR. 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.* 5:18–32

Schmitz OJ, Hambäck PA, Beckerman AP. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am. Nat.* 155:141–53

Schwartz MK, Mills LS, Ortega Y, Ruggiero LF, Allendorf FW. 2003. Landscape location affects genetic variation of Canada lynx (*Lynx canadensis*). *Mol. Ecol.* 12:1807–16

Seagle SW. 2003. Can deer foraging in multiple-use landscapes alter forest nitrogen budgets? *Oikos* 103:230–34

Soranno PA, Hubler SL, Carpenter SR, Lathrop RC. 1996. Phosphorus loads to surface waters: a simple model to account for spatial pattern of land use. *Ecol. Appl.* 6:865–78

Soranno PA, Webster KE, Riera JL, Kratz TK, Baron JS, et al. 1999. Spatial variation among lakes within landscapes: ecological organization along lake chains. *Ecosystems* 2:395–410

Spies TA, Ripple WJ, Bradshaw GA. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. *Ecol. Appl.* 4: 555–68

Steffan-Dewenter I, Munzenberg U, Burger C, Thies C, Tscharntke T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83:1421–32

Stoner KJL, Joern A. 2004. Landscape versus local habitat scale influences to insect communities from tallgrass prairie remnants. *Ecol. Appl.* 14:1306–20

Strayer DL, Beighley RE, Thompson LC, Brooks A, Nilsson C, et al. 2003a. Effects of land cover on stream ecosystems: roles of empirical models and scaling issues. *Ecosystems* 6:407–23

Strayer DL, Ewing HA, Bigelow S. 2003b. What kind of spatial and temporal details are required in models of heterogeneous systems? *Oikos* 102:654–62

Tallmon DA, Jules ES, Radke NJ, Mills LS. 2003. Of mice and men and trillium: cascading effects of forest fragmentation. *Ecol. Appl.* 13:1193–1203

Tewksbury JJ, Levey DJ, Haddad NM, Sargent S, Orrock JL, et al. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proc. Natl. Acad. Sci. USA* 99:12923–62

Tischendorf L. 2001. Can landscape indices predict ecological processes consistently? *Landsc. Ecol.* 16:235–54

Tongway DJ, Ludwig JA. 2001. Theories on the origins, maintenance, dynamics and functioning of banded landscapes. In *Banded Vegetation Patterning in Arid and Semiarid*

Environments: Ecological Processes and Consequences for Management. ed. D Tongway, C Valentin, J Segheri, pp. 20–31. New York: Springer-Verlag

Troll C. 1950. Die geographisched Landscahaft und ihre Erforschung. *Studium Generale* 3:163–81

Trzcinski MK, Fahrig L, Merriam G. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecol. Appl.* 9:586–93

Turner MG. 1989. Landscape ecology: the effect of pattern on process. *Annu. Rev. Ecol. Syst.* 20:171–97

Turner MG. 2005. Landscape ecology in North America: past, present and future. *Ecology* 86:1967–74

Turner MG, Gardner RH, O'Neill RV. 2001. *Landscape Ecology in Theory and Practice.* New York: Springer-Verlag. 401 pp.

Turner MG, Pearson SM, Bolstad P, Wear DN. 2003. Effects of land-cover change on spatial pattern of forest communities in the southern Appalachian Mountains (USA). *Landscape Ecol.* 18:449–64

Turner MG, Romme WH, Gardner RH, O'Neill RV, Kratz TK. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. *Landsc. Ecol.* 8:213–27

Turner MG, Tinker DB, Romme WH, Kashian DM, Litton CM. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). *Ecosystems* 7:751–75

Urban D, Goslee S, Pierce K, Lookingbill T. 2002. Extending community ecology to landscapes. *Ecoscience* 9:200–12

Urban DL, O'Neill RV, Shugart HH. 1987. Landscape ecology. *BioScience* 37:119–27

Vos CC, Verboom J, Opdam PFM, Ter Braak CJF. 2001.Toward ecologically scaled landscape indices. *Am. Nat.* 157:24–41

Wang H, Hall CAS, Cornell JD, Hall MHP. 2002. Spatial dependence and the relationship of soil organic carbon and soil moisture in Luquillo experimental forest. *Landsc. Ecol.* 17:671–84

Ward JV, Malard F, Tockner K. 2002. Landscape ecology: a framework for integrating pattern and process in river corridors. *Landsc. Ecol.* 17 (Suppl.):35–45

Wear DN, Bolstad P. 1998. Land-use changes in southern Appalachian landscapes: spatial analysis and forecast evaluation. *Ecosystems* 1:575–94

Wear DN, Turner MG, Flamm RO. 1996. Ecosystem management with multiple owners: landscape dynamics in a Southern Appalachian watershed. *Ecol. Appl.* 6:1173–88

Weller DE, Jordan TE, Correll DL. 1998. Heuristic models for material discharge from landscapes with riparian buffers. *Ecol. Appl.* 8:1156–69

Wells TC, Sheail J, Ball DF, Ward LK. 1976. Ecological studies on the Porton Ranges: relationships between vegetation, soils and land-use history. *J. Ecol.* 64:589–26

White D, Minotti PG, Barczak MJ, Sifneos JC, Freemark KE, et al. 1997. Assessing risks to biodiversity from future landscape change. *Conserv. Biol.* 11:349–60

Wickham JD, Riitters KH. 1995. Sensitivity of landscape metrics to pixel size. *Int. J. Remote Sens.* 16:3585–94

Wiens JA. 1999. The science and practice of landscape ecology. In *Landscape Ecological Analysis: Issues and Applications*, ed. JM Klopatek, RH Gardner, pp. 372–83. New York: Springer-Verlag

Wiens JA. 1976. Population responses to patchy environments. *Annu. Rev. Ecol. Syst.* 7:81–120

Wiens JA. 1989. Spatial scaling in ecology. *Funct. Ecol.* 3:385–97

Wiens JA, Crawford CS, Gosz JR. 1985. Boundary dynamics—a conceptual framework for studying landscape ecosystems. *Oikos* 45:421–27

Wiens JA, Moss MR, Turner MG, Mladenoff DJ, eds. 2005. *Foundation Papers in Landscape Ecology.* New York: Columbia Univ. Press. In press

With KA. 2002. The landscape ecology of

invasive spread. *Conserv. Biol.* 16:1192–03

With KA, King AW. 1997. The use and misuse of neutral landscape models in ecology. *Oikos* 79:219–29

With KA, Pavuk DM, Worchuck JL, Oates RK, Fisher JL. 2002. Threshold effects of landscape structure on biological control in agroecosystems. *Ecol. Appl.* 12:52–65

Wu J, Hobbs RJ. 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. *Landsc. Ecol.* 17:355–65

Wu J, Loucks OL. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Q. Rev. Biol.* 70:439–66