2

Causes and Consequences of Spatial Heterogeneity in Ecosystem Function

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Abstract

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

Introduction

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

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

Landscape ecology explicitly addresses the importance of spatial configuration for ecological processes (Turner et al. 2001), and, in North America, landscape studies were strongly promoted by ecosystem ecologists (Risser et al. 1984). Landscape ecology often, but not always, focuses on spatial extents that are much larger than those traditionally studied in ecosystem ecology. Early research in landscape ecology emphasized methods to describe and quantify spatial heterogeneity, spatially explicit models to relate pattern and process, and understanding of scale effects. Indeed, there are numerous metrics for quantifying spatial heterogeneity (e.g., Baskent and Jordan 1995; McGarigal and Marks 1995; Gustafson 1998; Gergel and Turner 2002), although the functional interpretation of pattern metrics has proved challenging (Turner et al. 2001). From landscape studies, ecology has gained new insights into how disturbances create and respond to landscape pattern and of population dynamics on heterogeneous landscapes. However, with a few exceptions, the consideration of ecosystem function has poorly been represented. This is surprising, given the initial strong links from ecosystem to landscape ecology (e.g., Risser et al. 1984; Turner 1989). In this paper, we (1) present an organizing framework that clarifies consideration of ecosystem processes in heterogeneous landscapes; (2) consider when spatial heterogeneity is important; (3) discuss methods for incorporating spatial heterogeneity in ecosystem function; and (4) identify challenges and opportunities for progress.

When Does Space Matter? A Conceptual Framework

Ecosystem processes are heterogeneous. The basic causes of this 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 processes vary with the biotic assemblage, disturbance events (including long-term legacies), and the activities of humans (Chapin et al. 1996; Amundson and Jenny 1997). However, despite this recognition, most ecosystem ecologists have focused on knowing the mean rates, in spite of the "noise" that results from spatial heterogeneity.

Organizing Ecosystem Processes

We suggest distinguishing between two general classes of ecosystem process when considering ecosystem function in heterogeneous landscapes. *Point processes* represent rates measured at a particular location (Figure 2.1a). Lateral transfers are assumed to be small relative to the measured response and are ignored. Examples of point processes include site-specific measurements of net primary production, net ecosystem production, denitrification, or nitrogen mineralization. *Lateral transfers* are flows of materials, energy, or information from one location to another represented in a two-dimensional space (Figure 2.1b). Examples of lateral transfers include the flow of nitrogen or phosphorus from land to water or the movements of nutrients across a landscape by herbivores.

Spatial heterogeneity can be considered in both the drivers and the ecosystem response variables (Figure 2.2). For the drivers, one can consider the spatial heterogeneity of the template—which often is multivariate—and of spatial processes, such as disturbance, that alter the template (Foster et al. 1998). For the process, one can consider the spatial pattern of occurrence

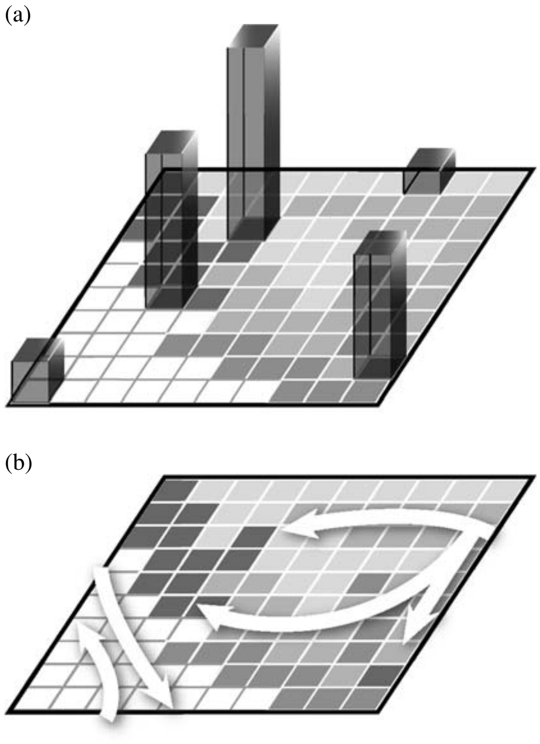

FIGURE 2.1. Schematic illustration of two general classes of ecosystem processes: (a) point processes and (b) lateral transfers.

(e.g., where denitrification does or does not occur or where there is nutrient movement; Figure 2.2a) or of the magnitude of the rates (Figure 2.2b). For lateral transfers, one can consider the actual pathways of flow (Figure 2.2b). For both point processes and lateral transfers, an aggregate measure of the function of the heterogeneous system (e.g., total P input to a lake) can be considered. When seeking general relationships, it is important to be explicit about both the type of ecosystem process being considered and the variable or response for which spatial heterogeneity is being considered.

When Is Spatial Heterogeneity Important?

Understanding the relationship between spatial heterogeneity and ecosystem processes is important in at least the following five situations.

(1) For point processes, spatial heterogeneity matters when it is necessary to know the average rate of a process over an area that is spatially heterogeneous. This is of particular importance when there is a nonlinear relationship between the process and a driver that is spatially variable. Although

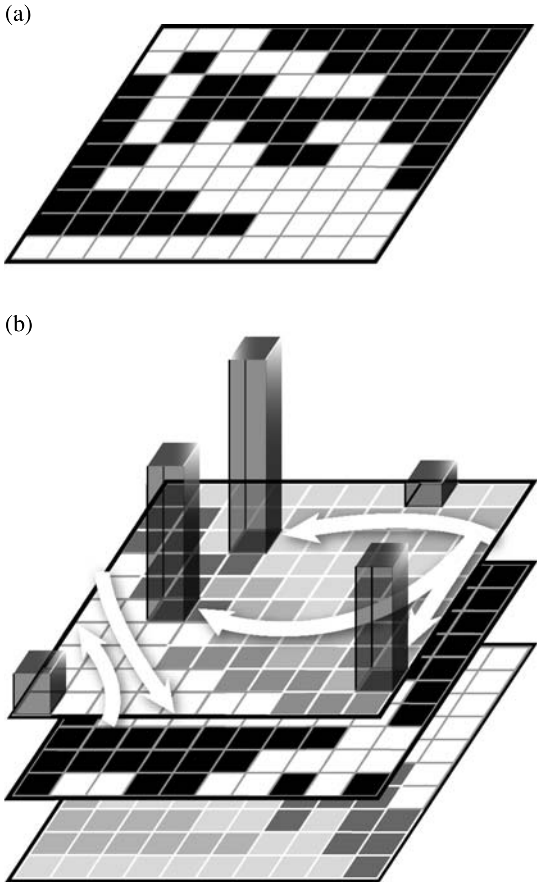

FIGURE 2.2. Spatial heterogeneity can be considered in (a) the occurrence of a process, (b) the magnitude of the rate or flux and the template, which is usually multivariate.

this is largely a sampling issue—knowing how to stratify measurements spatially based on the important driver(s)—it is not trivial.

Estimating methane production from a Siberian landscape that is a mosaic of land and lakes provides an example (Zimov et al. 1997). Lakes dominate the flux of methane within the landscape, but there is substantial heterogeneity of CH_4 flux within lakes. Bubbles of methane that form in ice over winter give visual evidence of hot spots of methane release from sediments. Here, the ebullition flux is several orders of magnitude larger than the diffusive flux, which is the main pathway of CH_4 flux between areas of bubbling. Therefore, to estimate the CH_4 flux from the lake, one must be aware of these different pathways and the spatial distribution of areas of ebullition. These hot spots dominate the fluxes of methane within the lake, and lakes, in turn, dominate fluxes from landscapes. Estimates of the average rate of methane flux from this landscape would be inaccurate if the spatial heterogeneity was ignored. This general class of problems is of great practical importance; ecosystem ecologists remain challenged by developing regional and global budgets for carbon and nutrient fluxes in heterogeneous regions.

(2) Spatial heterogeneity matters when one wants to understand or predict the spatial pattern of process rates. In so doing, one may want to identify locations that are qualitatively different in their processing rates from other areas, or use the spatial pattern or spatial scale of variation as a response variable of direct interest.

Understanding and predicting the spatial pattern of aboveground net primary production (ANPP) following the 1988 fires in Yellowstone National Park, Wyoming, provides an example. Postfire lodgepole pine densities varied from 0 to $>$500,000 stems ha^{-1} in response to spatial variation fire severity and in pre-fire serotiny within the stand, rather than from variation in soils, topography, or climate (Turner et al. 2004). In turn, ANPP varied from 1 to 15 Mg ha^{-1} yr^{-1} 10 years after the fires and was explained primarily by lodgepole pine sapling density. Compared to "classic" curves of NPP through time (e.g., depicted by Ryan et al. 1997 for spruce in Russia), these patterns indicate that the spatial variation observed in a single age class can equal or exceed the range of mean ANPP through successional time.

The spatial pattern or scale of variation in a process rate may be more informative than the mean, but few studies have explored this. Approaches derived from spatial statistics can be particularly useful in evaluating the scale of spatial variation. For example, the importance of land-use legacies for contemporary forest ecosystems has received increasing attention (e.g., Pearson et al. 1998; Foster et al. 1999; Currie and Nadelhoffer 2002; Dupouey et al. 2002; Mitchell et al. 2002; Turner et al. 2003). Fraterrigo et al. (2005) used a cyclic sampling design derived from spatial statistics (Clinger and Van Ness 1976) to determine whether prior land use influenced the spatial variability of soil chemical properties. Cyclic sampling designs use a repeated pattern of sampled plots that minimizes the number of samples but provides sample pairs separated by any distance (Burrows et al. 2002). Thus, this design is efficient for analyses such as semivariograms, correlograms, and spatial regression. Fraterrigo et al. (2005) hypothesized that soil properties would vary over fine scales in old-growth forest and over coarse scales in areas of past agriculture, which would have homogenized local variation. Results showed that prior land use did homogenize the variability in forest soils, and that the scales of variation for several response variables depended on past land use as hypothesized.

(3) If the occurrence or rate of a lateral transfer responds directly to spatial heterogeneity, then the spatial pattern (composition and configuration) becomes one of the independent variables in the analysis. Many examples can be found in studies of the flux of nutrients from upland to aquatic

ecosystems (e.g., Richards et al. 1996; Johnson et al. 1997; Jones et al. 2001). For example, the amount and arrangement of crop fields and riparian forests influences the delivery of nitrogen and phosphorus to streams (Peterjohn and Correll 1984; Reed and Carpenter 2002). Both the amount and spatial arrangement of land cover types must be considered to predict nutrient delivery. On boreal shield ridges in northwestern Ontario, the spatial arrangement of *Pinus mariana-Pinus banksiana* forest islands relative to patches of lichen, moss, and grass influenced N retention in a 2-yr NO_3 addition study (Lamontagne and Schiff 1999). These patches have characteristically different N cycles, with the forest patches being N limited and the lichen patches N saturated; the location of patches in the landscape was important for N export from the catchment.

(4) Spatial heterogeneity may also generate lateral transfers. For example, clearing of natural vegetation for agriculture in western Australia created a new landscape pattern that altered climate. A large block of newly cleared agricultural land was separated from the original heath vegetation by a rabbit fence, producing a new patch type that had a higher albedo and therefore absorbed less solar radiation than the adjacent heath (Chambers 1998). The greater sensible heat flux of the darker native heath vegetation caused the surface air to warm, become more buoyant, and rise. The rising air over the heath was replaced by moist air advected from the adjacent croplands, which in turn was replaced by dry subsiding air from aloft. Thus, the changes in spatial heterogeneity produced a small-scale circulation cell, analogous to a land-sea breeze, that increased precipitation by 10% over the heathlands and reduced it by 30% over the croplands, fundamentally changing this landscape. At a finer spatial scale, the juxtaposition of substrates with different C:N ratios, such as carbon-rich straw adjacent to nitrogen-rich mineral soil, may result in nutrient transfers (Mary et al. 1996). Fungi transport nitrogen to the log so they can produce enzymes to decompose the log. In these examples, spatial configuration is actually producing flows, which otherwise would not have occurred. Thus, understanding spatial heterogeneity is fundamental to understanding these lateral transfers and point processes.

(5) Finally, lateral transfers may produce, amplify, or moderate heterogeneity in patterns. The Alaska coastal current is an example of lateral transfers creating patterns. Ocean waters flow counterclockwise parallel to the coast while fresh water, derived from orographic precipitation as moist marine air strikes the coastal mountains, flows from the land to the ocean. This produces two relatively distinct and stable water masses: a low-density (warm, low salinity), low-nutrient fresh water mass that is adjacent to and above a dense eutrophic ocean water mass (Royer 1981). The front between these two water masses generates conditions that maximize productivity of phytoplankton, zooplankton, and fish. At this boundary, the oligotrophic ocean water provides nutrients, and the sharp density gradient minimizes vertical mixing of phytoplankton out of the photic zone. This boundary is

readily visible from the air from the high chlorophyll content and the concentration of foraging sea birds at the frontal zone. Spatial heterogeneity is a direct consequence of lateral flows.

The lateral transfers of nutrients by animals can also produce spatial patterns in nutrient pools, cycling rates, and productivity. Anadromous fish transport large quantities of marine-derived nutrients to streams and lakes. Otters, bears, and other piscivores move these nutrients to riparian forests, where they can contribute substantially to productivity (Willson et al. 1998; Naiman et al. 2002). The characteristic ^{15}N signature of marine-derived nitrogen is often detectable up to a kilometer from the river, suggesting a broad corridor of lateral nutrient transfer adjacent to streams with anadromous fisheries. Grazing ungulates also contribute to lateral nutrient transfers. In Switzerland, for example, the patchy distribution of cattle generated sharp nutrient gradients between forests and fields (Schutz et al. 2000). When cattle grazing ceased in national parks, these nutrient gradients became less pronounced, as native ungulates slowly redistributed these nutrients into the forests. Even random lateral movements that differ between predators and prey can generate spatial heterogeneity in ecosystem processes (Pastor, this volume).

Approaches for Dealing with Spatial Heterogeneity

Given that spatial heterogeneity is frequently important but poorly quantified, how should we begin to incorporate it into ecosystem studies? Shugart's (1998) classification of ecosystem models is also a useful classification for our discussion; we also acknowledge a similar classification of models in Baker's (1989) review of models of landscape change.

Homogenous Space

The simplest approach has been to assume homogeneity in rates across space—every point can be represented by the mean value of the rate (Figure 2.3a). Although this book focuses on spatial heterogeneity, the assumption of spatial homogeneity remains a valuable starting point or null model. This assumption is particularly useful for approximating pools or fluxes to order of magnitude; for some spatial extrapolations; and when physically averaging a response variable across variability at finer scales than the scale of interest.

Some processes can be extrapolated to large scales without explicitly considering landscape interactions. The extrapolation of carbon flux, for example, may adequately be represented in the short term from an understanding of its response to climate, vegetation, and stand age (Chapin et al. 2002: 329). The simulation of global net ecosystem production (NEP) by the terrestrial

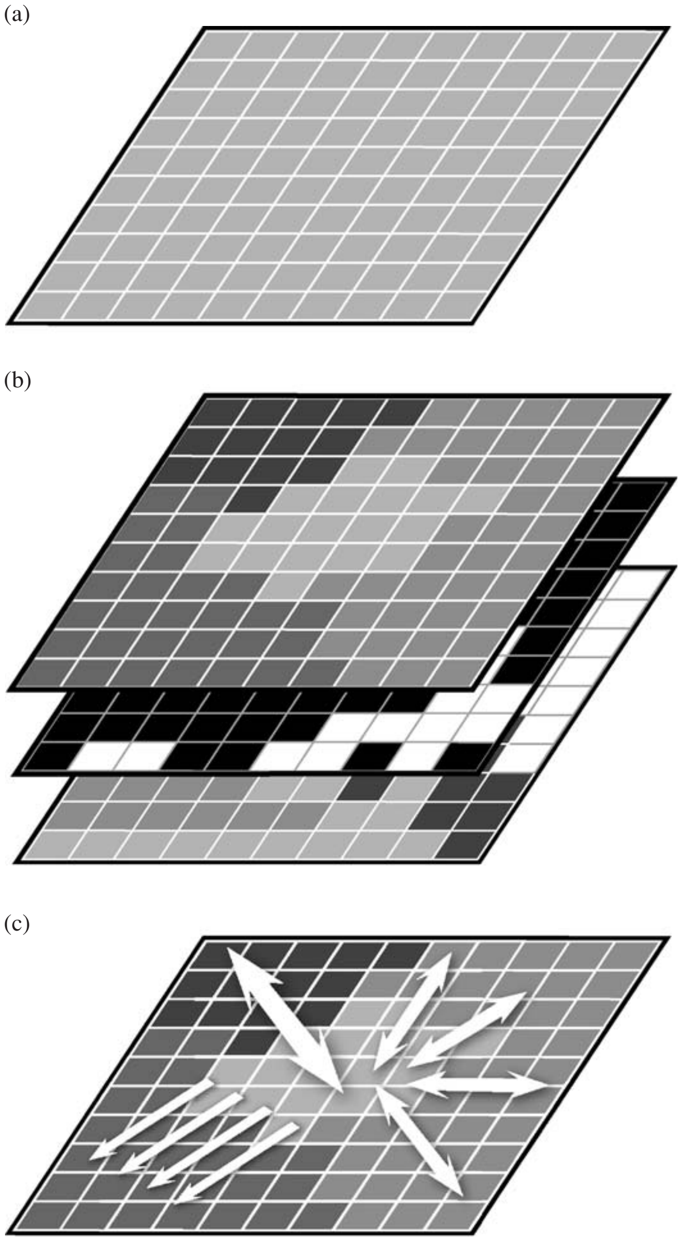

FIGURE 2.3. Three general approaches to dealing with space: (a) assuming spatial homogeneity, (b) the mosaic approach, which is often multivariate, and (c) interacting elements.

ecosystem model (TEM; McGuire et al. 1995) assumes homogeneity of environmental response within biomes to predict global patterns of NEP. This assumption allows the development of global databases even in areas where information is sparse or absent. Comparison of the output of these carbon flux models with seasonal and spatial patterns of atmospheric CO_2 identifies areas where assumptions of homogeneity are least justified and where additional information on spatial heterogeneity is most needed.

Eddy flux towers physically average measurements over an area of about 1 km^2. The heterogeneity in carbon fluxes resulting from fine-scale variation in soil aeration and other important ecosystem controls within the tower footprint is invisible because of the physical mixing of air. Consequently, the towers provide an accurate integration of the overall flux from the ecosystem (Davidson et al. 2002). These integrated landscape measures may be more useful than fine-scale information if extrapolation to large areas is based on satellite imagery that cannot resolve the fine-scale detail in ecosystem controls. Similarly, ecosystem ecologists frequently measure soil parameters and microbial processes on composite samples that physically average much of the fine-scale heterogeneity present in the ecosystem.

Of course, understanding the situations in which the assumption of spatial heterogeneity is likely to fail is important. Smithwick et al. (2003) used a forest process model to explore the assumption that carbon dynamics can be modeled within homogenous patches (e.g., even-aged forest stands) and then summed to predict broad-scale dynamics. Their results suggested that the additive approach might not capture C dynamics in fragmented landscapes because of edge-induced effects on tree mortality (primarily due to wind) and light limitations (Smithwick et al. 2003). This study nicely illustrates a systematic approach for identifying the conditions under which the assumption of spatial heterogeneity may produce erroneous conclusions.

Mosaics

Spatial mosaics are the simplest representation of spatial heterogeneity in ecological processes (Figure 2.3b). Mosaics are particularly useful for documenting and predicting spatial heterogeneity in point processes and for spatial extrapolation. It is important to recognize that the mosaic represents not only vegetation or land-cover types; more often, it is a complex multivariate mosaic of underlying controls. The rate of a process at a given location may depend on many factors, such as vegetation type, soil conditions, slope, aspect, elevation, or time since disturbance.

Mosaic effects on ecosystem processes can be represented using a "paint-by-numbers" approach that assumes no interaction among spatial elements. However, this approach is not trivial; it can be very complicated when the relationship is nonlinear, there are multiple drivers of a process, or the distributions of drivers change through time. Practically, regression or classification and regression tree (CART) techniques are often used with empirical data for this approach, with the relationship between a process rate and its drivers represented at each location across a landscape. The most common representation of spatial mosaics is a raster, or grid-cell, approach with resolution (or grain size) appropriate for the process of interest (Turner et al. 2001). Employing this approach requires knowing the spatial distribution of each driver. However, the prediction for each site is based only on the suite of independent variables associated with that location. Ecosystem simulation models can also be used to make predictions across a landscape mosaic. For example, Running et al. (1989) combined simulation models with remotely sensed data to predict photosynthesis, leaf area index, and evapotranspiration rate in grid cells representing the landscape of western Montana.

Many studies in which ecosystem process rates are extrapolated spatially use a mosaic approach. For example, Hansen et al. (2000) predicted rates of ANPP over the western portion of the Greater Yellowstone Ecosystem using a multiple regression model in the mosaic; Turner et al. (2004) used multiple regression within the areas of the 1988 Yellowstone fires to predict spatial variation in ANPP and leaf area index (LAI) within the burn. Similar approaches have been used for nitrogen mineralization rates (Fan et al. 1998), denitrification rates (Groffman et al. 1992), and other responses.

A mosaic approach may employ static or dynamic representations of spatial patterns. In the latter case, model estimates at each time step must account for any changes in spatial pattern that have occurred in at least one driver. These changes in pattern may result from feedbacks between the rate of the ecosystem process being measured or predicted and the occurrence of events that alter the pattern of the drivers—fire is an example of this. The point process rate, however, is still predicted without considering neighbors.

An "advanced paint-by-numbers" approach considers the context of the landscape surrounding a point at which measurements are made. This variant of the paint-by-numbers approach uses the characteristics of the point and the surrounding landscape (i.e., the landscape context) to determine the behavior of a point. In this case, the spatial distribution/pattern of each of the important driving variables must be known. The predicted value at a given site depends not only on the values of the predictor variables at that site, but also on the values of predictor variables in the surrounding area. There is a large literature using this approach to understand the effects of landscape context on the presence and/or abundance of organisms (e.g., Pearson 1993; Mazerolle and Villard 1999). The approach has also been useful in estimating ecosystem processes. For example, the concentration of dissolved organic carbon in lakes and rivers was predicted by the proportion of wetlands in the surrounding landscape (Gergel et al. 1999).

Ecosystem and landscape ecology have made reasonable progress in using the mosaic approach to represent variation in process rates, although the number of studies explicitly sampling for spatial variance remains relatively small. However, this approach is limited in its capacity to address dynamic space, complex feedbacks, or nonlinearities in responses. These components require a more dynamic consideration of interacting elements.

Interacting Elements

An interacting element approach is required to address lateral transfers. Typically, composition and configuration must both be considered. Ecosystem ecology does not yet have a comprehensive or even a well-developed approach for dealing with lateral transfers (Figure 2.3c). Empirical methods are frequently used to determine whether and when spatial pattern influences lateral transfer rates. Often, the response variable is an indicator of lateral transfer rather than a direct measurement of the transfer rate itself; for example, NO_3 concentration in soil water (e.g., lysimeter studies) may be used to track the movement and fate of N as it is transported from one ecosystem type to another. Labeled substances may be used as tracers to track directly the flow paths and rates or areas that differ in the composition and configuration of land cover types may be compared. Simulation models are also employed to predict the consequences of alternative spatial arrangements of cover types on lateral transfers. We consider three approaches of increasing complexity.

Static Spatial Pattern–Dynamic Lateral Transfers

The simplest approach to exploring the consequences of spatial pattern for lateral flows is to evaluate the consequences of a static landscape pattern on lateral transfers. This approach has been used particularly for studies of land-water interactions. Shaver et al. (1991), for example, tracked nutrient flows in a toposequence in Alaska based on the typical configuration of landscape elements. A comparative empirical approach can be used in which, for example, the spatial arrangements of land cover in a variety of watersheds is related to stream nutrient concentrations (e.g., Hunsaker and Levine 1995; Jones et al. 2001). The flows themselves are not measured directly, and concentration or loading is the index of magnitude of flow. Models are also helpful in this arena; for example, Weller et al. (1998) explored the effects of length, width, and number of gaps in a riparian buffer on nutrient delivery to a stream by using a simulation model. However, common to all of these approaches is the absence of feedback from the lateral transfer to the spatial pattern.

Dynamic Spatial Pattern–Dynamic Lateral Transfers

Here, spatial patterns are not stationary, and flows are assumed to respond to changes in the landscape template. Landscapes are constantly altered by natural disturbances and anthropogenic activities, and temporal changes in the spatial patterns of drivers can be represented. Horizontal flows respond to changes in these spatial patterns. For example, in the watershed of Lake Mendota, Wisconsin, land cover shifted from agricultural to urban uses between the 1930s and 1990s. The runoff of water from the terrestrial surface to the lake following storm events has become much more "flashy" during this period (Wegener 2001), illustrating how lateral transfers can respond to dynamic patterns over 60 years. Again, the lateral transfers do not alter the spatial pattern, but they respond to its temporal change.

Dynamic Spatial Pattern–Dynamic Lateral Transfers–Feedbacks Between Pattern and Process

Here, spatial patterns change, altering flows, which, in turn, alter the template itself. This complex set of relationships is perhaps most interesting, but poorly understood; again, both empirical and modeling approaches are informative. On Isle Royale, for example, moose (*Alces alces*) selectively browse on hardwood trees and balsam fir (*Abies balsamea*), which leads to domination of the landscape by conifers such as spruce. In turn, spruce domination alters patterns of productivity and nutrient cycling across the landscape, which then influences moose foraging patterns. These reciprocal interactions between moose and vegetation have been elucidated through a combination of intensive studies of moose movement and foraging patterns, vegetation dynamics, and nutrient cycling, along with models that explore the possible behaviors of the system (e.g., McInnes et al. 1992; Jeffries et al. 1994; Moen et al. 1997, 1998; Pastor et al. 1999). Similar complex relationships between ungulates and vegetation patterns have been observed in African landscapes (e.g., Seagle and McNaughton 1992; Augustine 2003).

In river-floodplain ecosystems, we also see reciprocal interactions between the water and the land. Floodplains and rivers are linked as integrated ecosystems through the exchange of particulate and dissolved matter (Tockner et al. 1999). The spatial patterns of geomorphology and vegetation in a floodplain can influence flooding and flow velocity, at least in years that are not extreme. Geomorphological and biological processes are inherently linked in a functional hierarchy (van Coller et al. 2000). A reciprocal interaction approach has also been used to model fire-vegetation in interior Alaska (Rupp et al. 2000, 2002). The landscape template (vegetation configuration and composition) determine both fire spread and subsequent seed dispersal and regeneration pattern. These processes, in turn, determine the vegetation template on the landscape, which influences fire probability and spread. Inclusion of these dynamic interactions allows an evaluation of potential impacts of external factors on either landscape pattern (e.g., land-use effects on vegetation pattern) or process (e.g., climate effects on fire probability). This dynamic approach is particularly important under circumstances where either pattern or process is undergoing directional change.

Challenges and Opportunities

If ecologists have recognized for 60 years that ecosystem processes are spatially heterogeneous (Jenny 1941), why is this topic relatively unexplored? We suggest there are several fundamental reasons then discuss some approaches for making sustained progress.

One challenge is that the interface between ecosystem and spatial ecology lacks a well developed theory (White and Brown, this volume). There is relatively little to guide us in our empirical studies, so our developing understanding has largely been empirical. However, even in empirical studies, the form of the relationship between response and driver variables is poorly understood and may well be nonlinear.

The technical sophistication and costs required to sample many ecosystem processes is relatively high. Sophisticated, expensive equipment is needed for many biogeochemical analyses, sample analysis is costly, and field sampling is labor-intensive. Adding the spatial dimension to a study design can substantially increase the number of samples needed. If a study attempts to understand spatial variance in rates over a large area, the logistics of conducting the sampling become quite challenging. As is true for many studies of broad-scale patterns, there are few opportunities to conduct experiments, although there are many opportunities for studying natural events or management actions from an experimental viewpoint. Even so, many people trained in ecosystem process studies lack advanced training in landscape ecology, spatial statistics, and spatially explicit models. Likewise, many people trained in landscape ecology lack the technical training in ecosystem ecology and biogeochemistry to address these questions.

Lack of understanding also results, in part, from inherent challenges related to variance and scale. For example, variance at fine spatial scales is extremely high for most biogeochemical processes, many of which are regulated by microorganisms. Relatively little is known about how microbial communities vary through both time and space. Because process rates may be measured at scales different from those of the controls, noise in the data can be overwhelming. Sampling adequately to obtain a general trend is already challenging without the added goal of understanding spatial variation.

Statistical considerations have also prompted ecosystem ecologists to avoid studies of spatial variation. In an effort to be rigorous, most ecosystem ecologists design observational or experimental studies that test for statistical differences between ecosystem types or treatments. This motivates experimental designs that minimize spatial variation (e.g., one- or two-way ANOVAs). Pastor (1995 and this volume) argues that this statistical preoccupation has done a disservice to ecosystem ecology, particularly modeling, where it is often more important to know the shape of a relationship between control and ecosystem response (e.g., between water availability and NPP) than to ask a simple yes/no question. Astute spatial sampling designs that incorporate heterogeneity in presumed control variables can provide valuable insights into nonlinearities and thresholds in controls over ecosystem processes that will never emerge from simple ANOVA designs.

Despite these challenges, there are ways to make progress, as described below.

Exploit Heterogeneity to Enhance Understanding of Processes

We urge ecologists to embrace spatial complexity and to treat it as an opportunity! Variance may be an important clue to our understanding of processes. For example, the fine-scale variation in microbial activity from one unit of soil to another could reflect important differences between processes within versus outside of soil aggregates, just as at larger scales we know that urine patches differ functionally from the matrix or that lakes differ from the terrestrial matrix. The extent to which ecosystem ecologists tend to think of heterogeneity as a nuisance rather than a reflection of important process controls is still problematic.

The spatial variability in tree N uptake within a small catchment was evaluated by Barker et al. (2002) by measuring major fluxes in the N cycle in 50 plots (20 m × 20 m). Results showed that overstory N uptake varied spatially in the watershed with stand structure, although the variance among different calculations was even greater. Nonetheless, uptake was correlated with stand structure. These results also underscore the intensive sampling required and some of the methodological challenges associated with estimating spatial structure in complex processes.

Conduct Studies at Multiple Scales

It is not possible to measure intensively everywhere, so sampling designs must be strategic. For example, intensive measurements at a small number of sites based on hypotheses can provide insights into mechanisms. However, these studies benefit from extensive measurements of simple integrative indices of these mechanisms at a larger number of sites to provide context. Nested sampling designs (Webster and Oliver 2001) are also useful. In addition, “smart” sampling designs derived from spatial statistics can maximize the power of the data. For example, a cyclic sampling design was used by Burrows et al. (2002) to maximize information about the variance of vegetation characteristics surrounding an eddy flux tower at Park Falls, Wisconsin. The data were also used to derive a spatial map of leaf area index (LAI) along with a map of spatial error measures for the study area (Burrows et al. 2002). Such methods afford the ability to quantify the scales of variation along with mean values of factors hypothesized to be important. Even though there is now a well developed statistical methodology to assess process controls at multiple scales, it has seldom been applied in ecosystem studies. The combination of intensive studies with spatially extensive measurements can also be used to see how well the knowledge at fine scales can be applied more broadly.

Use Empirical and/or Simulation Models for Extrapolation

Modeling can be a powerful tool for exploring the range of conditions under which a given set of process controls leads to plausible outcomes. The simulation results can then be tested against field observations. These extrapolations represent testable hypotheses about our understanding of the system, and they should be used more widely as such (Miller et al. 2004). For example, the extrapolation of a hypothesized relationship using paint-by-numbers can be tested in the field to determine the limits of the validity of this presumed relationship. Models provide context and permit exploration of more combinations of conditions than we can assess in the field. Statistical models can also be used to extrapolate to broad scales and can be tested with remote sensing data and/or extensive field measurements to see whether they are consistent with predictions.

Be Creative About When and How to Use Discrete versus Continuous Representations of Space

There are a variety of ways in which space may be represented in both drivers and response variables. The two most common representations of spatial heterogeneity include categorical maps and point data (Gustafson 1998). In categorical maps, variables are mapped in space, and both composition and configuration can be quantified. A wide variety of metrics is available to quantify such patterns (e.g., McGarigal and Marks 1995). Although categorical maps are often created from continuous data (e.g., forest cover is often mapped based on the proportion of a cell occupied by trees), this approach ignores spatial variation within the units (Gustafson 1998). Point-data analysis, in contrast, assumes the system property is spatially continuous, and an area is sampled to generate spatially referenced information about the system. Analysis techniques include trend-surface analysis, various techniques that address spatial autocorrelation (e.g., correlograms, semivariograms), and interpolation. Platt and Sathyendranath (1999) correctly note, however, that universal functions for continuous variation of environmental properties generally have not been discovered.

Careful consideration of how and why space should be represented is crucial, and the representation of heterogeneity should match the question and be scaled correctly. Point data are required for interpolation methods (e.g., kriging) or for using scales of variation as a response variable. However, a categorical approach might simplify the analysis of biogeochemical hot spots by eliminating the need to treat all variation in processing rates. For example, one might predict locations where a process like denitrification occurs in a floodplain (or where the rate exceeds some meaningful threshold) rather than predicting the actual rates. We echo Gustafson's (1998) plea for moving beyond the patch-based view of spatial heterogeneity and for recognition of the complementarity between categorical and continuous representations of space.

Collaborate and Explore Other Bodies of Theory

Intra- and interdisciplinary collaboration often produces new insights, and we encourage ecologists to look beyond their research specialty. What theories developed in other disciplines within or outside of ecology might be helpful? Percolation theory (Stauffer 1985; Stauffer and Aharony 1992), a branch of physics, offered new modeling and analysis techniques that were applied in landscape ecology (Gardner et al. 1987) and led to new insights about crucial thresholds in connectivity (With and King 1997). Within ecology, there is an extensive body of literature on source-sink dynamics for populations—might that theory be relevant for lateral transfers of matter or energy? Gases and particulates emitted from managed or natural ecosystems (sources) can be transported great distances, altering the recipient (sink) ecosystems. Boerner and Kooser (1989) studied redistribution of leaf litter within a 73-ha watershed in Ohio and used donor and sink terminology. Donor sites lost 4.5–5.7 ka ha^{-1} yr^{-1} of N and 0.3–0.5 kg ha^{-1} yr^{-1} of P through redistributed litter; sink areas received subsidies of 2.2–6.1 kg ha^{-1} yr^{-1} N and 0.2–0.4 kg ha^{-1} yr^{-1} of P. Pastor (this volume) also suggests that cross-fertilization between ecosystem ecology and evolutionary studies is likely to produce new understanding about ecosystem function in time and space.

Looking Ahead

Understanding spatial heterogeneity has been referred to as "the final frontier" in other areas within ecology (e.g., Kareiva 1994). Although new challenges will continually arise, understanding the causes and consequences of ecosystem function in heterogeneous landscapes is a challenge that will be present for some time. Methods to quantify spatial heterogeneity abound; gaining a functional understanding of spatial pattern should be the priority rather than the development of new pattern metrics. If knowledge of spatial heterogeneity and ecosystem function improves, it is appropriate to consider the significance of this enhanced understanding. There are at least three areas in which advances will be significant to our science.

First, understanding of pools, fluxes, and regulating factors in ecosystems will be enhanced—and this defines the purview of ecosystem ecology. By understanding heterogeneity, what causes it, and when it matters, we will have a much better understanding of fundamental ecosystem processes. Broad-scale estimates of biogeochemical processes, which are key for understanding regional to global phenomena, require spatial understanding (e.g., Groffman et al. 1992). Factors such as disturbance frequency and size, species distributions, and exotic species invasions that are inherently spatial may influence not only the magnitude but also the sign of currently observed ecosystem fluxes within the next century (Canadell et al. 2000). Second, we will gain a more complete understanding of landscape function. At present, there is greater knowledge about how certain populations respond to patterns, the role of disturbance dynamics, and even the perceptions and effects of humans. However, this list conspicuously excludes knowledge of ecosystem function in both natural and anthropogenic landscapes. Indeed, understanding spatial heterogeneity and disturbance is one of the key needs for global studies (Schimel et al. 1997). Third, the ability to scale up or down will be improved. Using spatial models and spatial extrapolations as hypotheses should help identify the domains through which certain relationships do and do not scale (Miller et al. 2004). Ultimately, these gains should lead to improved predictions of changes in regional systems that involve multiple feedbacks between pattern and process at multiple scales.

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References

Amundson, R., and Jenny, H. 1997. On a state factor model of ecosystems. BioScience 47: 536–543.

Augustine, D.J. 2003. Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. J. Appl. Ecol. 40: 137–149.

Baker, W.L. 1989. A review of models of landscape change. Landscape Ecol. 2: 111–133.

Barker, M., Van Miegrot, H., Nicholas, N.S., and Creed, I.F. 2002. Variation in overstory nitrogen uptake in a small, high-elevation southern Appalachian spruce-fir watershed. CJFR 32: 1741–1752.

Baskent, E.Z., and Jordan, G.A. 1995. Characterizing spatial structure of forest landscapes. Can. J. Forest Res. 25: 1830–1849.

Boerner, R.E.J., and Kooser, J.G. 1989. Leaf litter redistribution among forest patches within an Alleghany Plateau watershed. Landscape Ecol. 2: 81–92.

Burke, I.C., Lauenroth, W.K., Riggle, R., Brannen, P., Madigan, B., and Beard, S. 1999. Spatial variability of soil properties in the shortgrass steppe: the relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. Ecosystems 2: 422–438.

Burrows, S.N., Gower, S.T., Clayton, M.K., Mackay, D.S., Ahl, D.E., Norman J.M., and Diak, G. 2002. Application of geostatistics to characterize leaf area index (LAI) from flux tower to landscape scales using a cyclic sampling design. Ecosystems 5: 667–679.

Canadell, J.G., Mooney, H.A., Baldocchi, D.D., Berry, J.A., Ehleringer, J.R., Field, C.B., Gower, S.T., Hollinger, D.Y., Hunt, J.E., Jackson, R.B., Running, S.W., Shaver, G.R., Steffen, W., Trumbore, S.E., Valentini, R., and Bond, B.Y. 2000. Carbon metabolism of the terrestrial biosphere: a multitechnique approach for improved understanding. Ecosystems 3: 115–120.

Carpenter, S.R., and Turner, M.G. 1998. At last: a journal devoted to ecosystem science. Ecosystems 1: 1–5.

Carpenter, S.R., Ludwig, D., and Brock, W.A. 1999. Management of eutrophication for lakes subject to potentially irreversible change. Ecol. Applications 9: 751–771.

Chambers, S. 1998. Short- and long-term effects of clearing native vegetation for agricultural purposes. Ph.D. Thesis, Flinders University of South Australia, Adelaide, Australia.

Chapin III, F.S., Torn, M.S., and Tateno, M. 1996. Principles of ecosystem sustainability. Am. Naturalist 148: 1016–1037.

Chapin III, F.S., Matson, P.A., and Mooney, H.A. 2002. Principles of terrestrial ecosystem ecology. New York: Springer-Verlag.

Clinger, W., and Van Ness, J.W. 1976. On unequally spaced time points in time series. Ann. Stat. 4: 736–745.

Currie, W.S., and Nadelhoffer, K.J. 2002. The imprint of land-use history: patterns of carbon and nitrogen in downed woody debris at the Harvard Forest. Ecosystems 5: 446–460.

Davidson, E.A., Savage, K., Verchot, L.V., and Navarro, R. 2002. Minimizing artifacts and biases in chamber-based measurements of soil respiration. Agric. Forest Meteorol. 113: 21–37.

Dupouey, J.L., Dambrine, E., Laffite, J.D., and Moares, C. 2002. Irreversible impact of past land use on forest soils and biodiversity. Ecology 83: 2978–2984.

Fan, W., Randolph, J.C., and Ehman, J.L. 1998. Regional estimation of nitrogen mineralization in forest ecosystems using Geographic Information Systems. Ecol. Applications 8: 734–747.

Foster, D.R., Knight, D.H., and Franklin, J.F. 1998. Landscape patterns and legacies resulting from large infrequent forest disturbances. Ecosystems 1: 497–510.

Foster, D.R., Fluet, M., and Boose, E.R. 1999. Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. Ecol. Applications 9: 555–572.

Fraterrigo, J., Turner, M.G., Pearson, S.M., and Dixon, P. 2005. Effects of past land use on spatial heterogeneity of soil nutrients in Southern Appalachian forests. Ecological Monographs 75: 215–230.

Gardner, R.H., Milne, B.T., Turner, M.G., and O’Neill, R.V. 1987. Neutral models for the analysis of broad-scale landscape patterns. Landscape Ecol. 1: 19–28.

Gergel, S.E., Turner, M.G., and Kratz, T.K. 1999. Scale-dependent landscape effects on north temperate lakes and rivers. Ecol. Applications 9: 1377–1390.

Gergel, S.E., and Turner, M.G., eds. 2002. Learning landscape ecology: a practical guide to concepts and techniques. New York: Springer-Verlag.

Golley, F.B. 1993. A history of the ecosystem concept in ecology: more than the sum of the parts. New Haven, CT: Yale University Press.

Groffman, P.M., Tiedje, T.M., Mokma, D.L., and Simkins, S. 1992. Regional-scale analysis of denitrification in north temperate forest soils. Landscape Ecol. 7: 45–54.

Gustafson, E.J. 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems 1: 143–156.

Hansen, A.J., Rotella, J.J., Kraska, M.P.V., and Brown, D. 2000. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. Landscape Ecol. 15: 505–522.

Hunsaker, C.T., and Levine, D.A. 1995. Hierarchical approaches to the study of water quality in rivers. BioScience 45: 193–203.

Jeffries, R.L., Klein, D.R., and Shaver, G.R. 1994. Vertebrate herbivores and northern plant communities: reciprocal influences and responses. Oikos 71: 193–206.

Jenny, H. 1941. Factors of soil formation. New York: McGraw-Hill.

Johnson, L.B., Richards, C., Host, G., and Arthur, J.W. 1997. Landscape influences on water chemistry in midwestern streams. Freshwater Biol. 37: 209–217.

Jones, K.B., Neale, A.C., Nash, M.S., Van Remortel, R.D., Wickham, J.D., Riitters, K.H., and O'Neill, R.V. 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: 301–312.

Kareiva, P. 1994. Space: the final frontier for ecological theory. Ecology 75: 1.

Lamontagne, S., and Schiff, S.L. 1999. The response of a heterogeneous upland boreal shield catchment to a short term NO_3^- addition. Ecosystems 2: 460–473.

Mary, B., Recous, S., Darwis, D., and Robin, D. 1996. Interactions between decomposition of plant residues and nitrogen cycling in soil. Plant Soil 181: 71–82.

Mazerolle, M.J., and Villard, M.A. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience 6: 117–124.

McGarigal, K., and Marks, B.J. 1995. FRAGSTATS. Spatial analysis program for quantifying landscape structure. USDA Forest Service General Technical Report PNW-GTR-351.

McGuire, A.D., Melillo J.W., Kicklighter, D.W., and Joyce, L.A. 1995. Equilibrium responses of soil carbon to climate change: empirical and process-based estimates. J. Biogeogr. 22: 785–796.

McInnes, P.F., Naiman, R.J., Pastor, J., and Cohen, Y. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 75: 478–488.

Miller, J.R., Turner, M.G., Smithwick, E.A.H., Stanley, E.H., and Dent, L.C., 2004. Spatial extrapolation: the science of predicting ecological patterns and processes. Bio Science 54: 310–320.

Mitchell, C.E., Turner, M.G., and Pearson, S.M. 2002. Effects of historical land use and forest patch size on myrmecochores and ant communities. Ecol. Applications 12: 1364–1377.

Moen, R., Cohen, Y., and Pastor, J. 1997. A spatially explicit model of moose foraging and energetics. Ecology 78: 505–521.

Moen, R., Pastor, J., and Cohen, Y. 1998. Linking moose population and plant growth models with a moose energetics model. Ecosystems 1: 52–63.

Naiman, R.J. 1996. Water, society and landscape ecology. Landscape Ecol. 11: 193–196.

Naiman, R.J., Bilby, R.F., Schindler, D.E., and Helfield, J.M. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems 5: 399–417.

Pace, M.L., and Groffman, P.M., eds. 1998. Successes, limitations and frontiers in ecosystem science. New York: Springer.

Pastor, J. 1995. Diversity of biomass and nitrogen distribution among plant species in arctic and alpine tundra ecosystems. In Arctic and alpine biodiversity: patterns, causes and ecosystem consequences, eds. F.S. Chapin III, and C. Korner, pp. 255–269. Berlin: Springer-Verlag.

Pastor, J., Cohen, Y., and Moen, R. 1999. Generation of spatial patterns in boreal forest landscapes. Ecosystems 2: 439–450.

Pearson, S.M. 1993. The spatial extent and relative influence of landscape-level factors on wintering bird populations. Landscape Ecol. 8: 3–18.

Pearson, S.M., Smith, A.B., and Turner, M.G. 1998. Forest fragmentation, land use, and cove-forest herbs in the French Broad River Basin. Castanea 63: 382–395.

Peterjohn, W.T., and Correll. D.L. 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. Ecology. 65: 1466–75.

Platt, T., and Sathyendranath, S. 1999. Spatial structure of pelagic ecosystem processes in the global ocean. Ecosystems 2: 384–394.

Polis, G.A., and Hurd, S.D. 1996. Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am. Naturalist 147: 396–423.

Reed, T., and Carpenter, S.R. 2002. Comparisons of P-yield, riparian buffer strips, and land cover in six agricultural watersheds. Ecosystems 5: 568–577.

Richards, D., Johnson, L.B., and Host, G. 1996. Landscape-scale influences on stream habitats and biota. Can. J. Fisheries Aquatic Sci. 53(Suppl. 1): 295–311.

Risser, P.G., Karr, J.R., and Forman, R.T.T. 1984. Landscape ecology: directions and approaches. Special Publication Number 2. Champaign, IL: Illinois Natural History Survey.

Royer, T.C. 1981. Baroclinic transport in the Gulf of Alaska. Part II. A fresh water driven coastal current. J. Marine Res. 39: 251–266.

Running, S.W., Nemani, R.R., Peterson, D.L., Band, L.E., Potts, D.F., Pierce, L.L., and Spanner, M.A. 1989. Mapping regional forest evapotranspiration and photosynthesis by coupling satellite data with ecosystem simulation, Ecology 70: 1090–1101.

Rupp, T.S., Chapin, F.S., and Starfield, A.M. 2000. Response of subarctic vegetation to transient climatic change on the Seward Peninsula in northwest Alaska. Global Change Biology 6: 541–555.

Rupp, T.S., Starfield, A.M., Chapin III, F.S., and Duffy, P. 2002. Modeling the impact of black spruce on the fire regime of Alaskan boreal forest. Climatic Change 55: 213–233.

Ryan, M.G., Binkley, D., and Fownes, J.H. 1997. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. 27: 213–262.

Seagle, S.W., and McNaughton, S.J. 1992. Spatial variation in forage nutrient concentrations and the distribution of Serengeti grazing ungulates. Landscape Ecol. 7: 229–241.

Schimel, D.S., VEMAP Participants, and Braswell, B. H. 1997. Continental scale variability in ecosystem processes: models, data, and the role of disturbance. Ecol. Monogr. 67: 251–271.

Schutz, M., Krusi, B.O., Edwards, P.J., eds. 2000. Succession research in the Swiss National Park. National Park-Forschung in der Schweiz, No. 89.

Shaver, G.R., Knadelhoffer, K.J., and Giblin, A.E. 1991. Biogeochemical diversity and element transport in a heterogeneous landscape, the north slope of Alaska. In Quantitative methods in landscape ecology, eds. M.G. Turner, and R.H. Gardner, pp. 105–125. New York: Springer-Verlag.

Shugart, H.H. 1998. Terrestrial ecosystems in changing environments. Cambridge, UK: Cambridge University Press.

Smithwick, E.A.H., Harmon, M.E., and Domingo, J.B. 2003. Modeling multiscale effects of light limitations and edge-induced mortality on carbon stores in forest landscapes. Landscape Ecol. 18: 701–721.

Soranno, P.A., Webster, K.E., Riera, J.L., Kratz, T.K., Baron, J.S., Bukaveckas, P.A., Kling, G.W., White, D.S., Caine, N., Lathrop, R.C., and Leavitt, P.R. 1999. Spatial variation among lakes within landscapes: ecological organization along lake chains. Ecosystems 2: 395–410.

Stauffer, D. 1985. Introduction to percolation theory. London: Taylor & Francis.

Stauffer, D., and Aharony, A. 1992. Introduction to percolation theory, 2nd ed. London: Taylor & Francis.

Tockner K., Pennetzdorfer, D., Reiner, N., Schiemer, F., and Ward, J.V. 1999. Hydrological connectivity, and the exchange of organic matter and nutrients in a dynamic river floodplain system (Danube, Austria). Freshwater Biol. 41: 521–535.

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Systematics 20: 171–197.

Turner, M.G., Gardner, R.H., and O'Neill, R.V. 2001. Landscape ecology in theory and practice. New York: Springer-Verlag.

Turner, M.G., Romme, W.H., Tinker, D.B., and Kashian, D.M. 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems 7: 751–775.

Turner, M.G., Pearson, S.M., Bolstad, P., and Wear. D.N. 2003. Effects of land-cover change on spatial pattern of forest communities in the southern Appalachian Mountains (USA). Landscape Ecol 18: 449–464.

van Coller, A.L., Rogers, K.H., and Heritage, G.L. 2000. Riparian vegetation–environment relationships: complementarity of gradients versus patch hierarchy approaches. J. Veg. Sci. 11: 337–350.

Webster, R., and Oliver, M.A. 2001. Geostatistics for environmental scientists. Chichester, UK: John Wiley & Sons, Ltd.

Wegener, M.W. 2001. Long-term land use/cover change patterns in the Yahara Lakes region and their impact on runoff volume to Lake Mendota. M.S. Thesis, University of Wisconsin, Madison, WI.

Weller, D.E., Jordan, T.E., and Correll, D.L. 1998. Heuristic models for material discharge from landscapes with riparian buffers. Ecol. Applications 8: 1156–1169.

Willson, M.F., Gende, S.M., and Marston, B.H. 1998. Fishes and the forest. BioScience 48: 455–462.

With, K.A., and King, A.W. 1997. The use and misuse of neutral landscape models in ecology. Oikos 97: 219–229.

Zimov, S.A., Voropaev, Y.V., Semiletov, I.P., Davidov, S.P., Prosiannikov, S.F., Chapin III, F.S., Chapin, M.C., Trumbore, S., and Tyler, S. 1997. North Siberian lakes: a methane source fueled by Pleistocene carbon. Science 277: 800–802.