Multiscale Organization of Landscape Heterogeneity

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ABSTRACT

Environmental heterogeneity is hierarchical and is controlled by different processes at different spatial and temporal scales. Recent studies have demonstrated the existence of pattern within nested discrete scales on natural landscapes. A disturbance that disrupts this structure could have far-reaching ecological consequences; however, natural disturbance-recovery regimes often create and maintain spatial and temporal heterogeneity in landscapes. A broad framework for the description of landscapes that separates the spatial from the temporal scales of disturbance and recovery can be used to predict the resultant dynamics of a landscape. This framework permits the prediction of disturbance conditions that lead to qualitatively different landscape dynamics and demonstrates the scale-dependent nature of landscape equilibrium.

Results from numerous studies suggest that landscape connectivity is important to many ecological processes. Connectivity can change rapidly when landscape heterogeneity is altered, thereby, indicating the existence of critical thresholds. Critical thresholds in habitat abundance and connectivity can be identified for a variety of organisms, but the values of these thresholds differ with both the landscape pattern and the scale at which an organism can use the landscape. It is most difficult to predict the consequences of altered landscape patterns at intermediate levels of habitat abundance because of complex interactions between pattern and scale or resource utilization by different organisms. Suggestions for maintaining landscape heterogeneity at multiple scales are presented.

INTRODUCTION

Describing environmental heterogeneity is challenging because heterogeneity occurs at various spatial and temporal scales and is controlled by a diverse set of processes. In this paper, we discuss the hierarchical nature of environmental heterogeneity, the implications of scale-dependence for disturbance dynamics, and the consequences of landscape patterns. We also propose general concepts for land management based on the implications of the multiscale organization of landscapes.

Multiscale Heterogeneity in Landscapes

Environmental heterogeneity is hierarchical (Allen and Starr 1982, O'Neill et al. 1986, Urban et al. 1987) and is controlled by different processes at different spatial and temporal scales (Delcourt et al. 1983). The spatial distribution of life zones on a continent, for example, is controlled by climatic factors such as precipitation and temperature (Raunkaier 1934, Whittaker 1956). Within a life zone, however, the vegetation present at a particular location varies with soil type and topography; for example, landscapes in the southern Appalachian mountains are dominated by deciduous forest, but different species assemblages are characteristic of different topographic positions. Within a given soil type and topographic condition, tree density, stand age structure, and species composition also may vary due to disturbance history.

Recent studies have tested this hierarchical paradigm and demonstrated the existence of discrete scales of pattern on the landscape. O'Neill and others (1991), following a suggestion of Levin and Buttel (1986), examined six grassland and forested landscapes. By graphing an estimation of variance against spatial extent of the sample, Levin and Buttel demonstrated that a multiscale structure existed on four of the landscapes. O'Neill and others (1992) used spatial analysis of transect data to demonstrate three to five distinct scales of pattern on three landscapes. Later efforts confirmed this result for four additional landscapes (O'Neill et al., unpublished). Hierarchical patterning in resources could affect consumer communities. An indirect demonstration of multiple scales was published by Holling (1992). He reasoned that if resources showed distinct scales, then the size of consumer home ranges would depend on these resource scales. Following McNab (1963), Holling suggested that discontinuities in the statistical distribution of home-range sizes would appear as clusters of body sizes in vertebrates. By examining existing data sets, he was able to establish the hypothesized clustering of body sizes. Holling also provides an extensive discussion of the endogenous and exogenous processes that generate these spatial scales.

Although the terms patch, matrix, and corridor commonly are used in landscape ecology, a rigid interpretation of these terms can impede our understanding of multiscale heterogeneity (Turner et al., in press). These terms are most useful when there is high contrast between patch and matrix (e.g., agricultural fields in a forested region) and this contrast is ecologically meaningful. It is difficult, however, to define patches in a landscape without being arbitrary. Through an organism-based perspective, patches have been defined in an ecological context as a discontinuity in an ecological variable affecting an organism (Wiens 1986). Analyzing landscape heterogeneity at the scale of an organism, especially a nonvertebrate, can reveal strikingly different environmental patterns and gradients than those apparent to humans (e.g., Buechner 1989, Wiens 1989, Wiens and Milne 1989). For instance, landscape connectivity (i.e., the degree to which sites are contiguous) will be perceived differently by an ant and an eagle.

Multiscale patterning is the result of interacting physical and biological phenomena. Landscape heterogeneity often is produced and maintained by ecosystem disturbance and recovery dynamics. The resulting patterns have consequences for several ecological processes at the landscape scale. Recognizing these patterns of heterogeneity, as well as their causes and consequences, is necessary for developing management plans consistent with preserving the ecological integrity of landscapes.

Disturbances and Hierarchies: The Implications of Scale Dependence

Because a landscape appears to be organized as a hierarchy of discrete spatial scales of pattern, it seems likely that any disturbance disrupting this structure could have far reaching ecological consequences. Such a disturbance might disrupt the scale of pattern in the spatial distribution of resources and could eliminate an entire component of the consumer community that depends on the scale of resource distribution affected. Thus, activities such as clearcutting or urbanization can substantively alter the natural hierarchical structure of a landscape.

Natural disturbance-recovery regimes often create and maintain spatial and temporal heterogeneity in landscapes. Natural disturbances often exhibit characteristic scales in time and space. Turner and others (in press) developed a broad framework for the description of landscapes that separates the spatial and temporal scales of disturbance, thereby allowing time and space to be considered separately. Four major factors characterizing the scale dynamics of landscapes are considered: (1) disturbance frequency, as indicated by the interval between successive disturbances (e.g., Baker 1989a, 1989b, Romme 1982); (2) rate of recovery from disturbance, as indicated by the length of time required for a disturbed site to recover (e.g., Pickett and White 1985); (3) the size or spatial extent of disturbance events (e.g., Baker 1989a, 1989b, Bormann and Likens 1979, Romme 1982; Shugart and West 1981); and (4) the size or spatial extent of the landscape (e.g., Baker 1989a and 1989b, Shugart and West 1981). These factors are then reduced to two key parameters representing time and space to describe potential disturbance dynamics.

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

The spatial parameter (S) is defined by the ratio of the size of the disturbance to the size of the landscape. There are two qualitatively different states of importance here, again regardless of the type of disturbance: disturbances that are large relative to the size of the landscape, and disturbances that are small relative to the extent of the landscape. As defined in this paper, the parameter S can range from 0 to 1. Landscape dynamics cannot be predicted if the size of the disturbance exceeds the spatial extent of the landscape because the landscape is too small to characterize the effect and recovery from disturbance.

The use of ratios in both parameters permits the comparison of landscapes across a range of spatial and temporal scales. We use the parameters to describe a landscape state-space in which the temporal parameter is placed on the Y axis, and the spatial parameter is displayed on the X-axis (fig. 1).

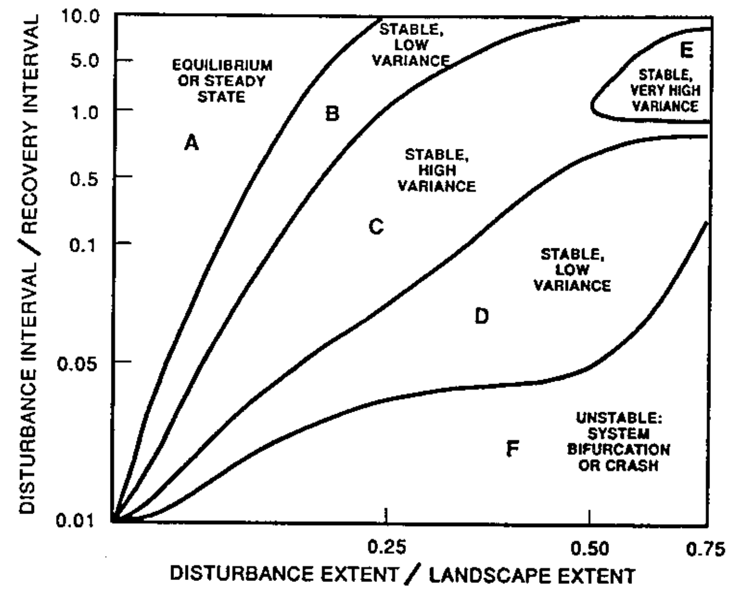

Figure 1--State-space diagram of temporal and spatial parameters that illustrate regions with qualitatively different landscape dynamics (from Turner et al., in press).

A simple simulation model was developed to explore the implications of various combinations of S and T. Results indicate (fig. 1) that where disturbance interval is long relative to recovery time, and a small proportion of the landscape is affected, the system is stable and exhibits low variance over time (e.g., northeastern hardwood forests). These systems are traditionally considered to be in "equilibrium". Where disturbance interval is comparable to recovery interval and a large proportion of the landscape is affected, the system is stable but exhibits large variance (e.g., subalpine forests in Yellowstone Park). Where disturbance interval is much shorter than recovery time, and a large proportion of the landscape is affected, the system may become unstable and shift into a different trajectory (e.g., arid ecosystems with altered fire regimes). This framework permits the prediction of disturbance conditions that lead to qualitatively different landscape dynamics and demonstrates the scale-dependent nature of landscape equilibrium.

Scale-dependent disturbance dynamics have several important implications for land management. First, there is no spatial extent that can guarantee landscape equilibrium. Increasing spatial extent should, however, decrease the probability of a dramatic shift in landscape dynamics due to a rare disturbance event. Second, if the temporal or spatial scale of disturbance regimes are altered sufficiently (e.g., by climate change or land management), dramatic changes in landscape patterns are likely. Past climatic changes of small magnitude have caused significant changes in fire regimes in forested landscapes (Clark 1988, Hemstrom and Franklin 1982). Global warming may result in an increase in the frequency of dry years and, hence, an increase in the size or frequency of fire (Flannigan and Harrington 1988, Romme and Turner 1991, Sandenburgh et al. 1987). One could explore the implications of changes in a disturbance regime by locating the current position of a landscape in figure 1, then plotting a potential position within the state-space under a new disturbance regime. In this manner, the potential for a qualitative shift in landscape dynamics (e.g., from equilibrium to stable with high variance) could be identified. A landscape might, however, sustain a substantial change in disturbance regime, but remain within the same region of dynamics. Third, results of our model demonstrate the scale-dependent nature of landscape equilibrium. Conclusions regarding the apparent stability of a landscape are appropriate only for a specified spatial and temporal scale. Failure to recognize scale dependence can lead to sharply different interpretations about the same dynamics.

Consequences of Landscape Patterns

Spatial patterns in the landscape may influence a variety of ecological phenomena (Turner 1989) such as the distribution and persistence of populations (Fahrig and Paloheimo 1988, Van Dorp and Opdam 1987), the horizontal flow of materials such as sediment or nutrients (Kesner and Meentemeyer 1989, Peterjohn and Correll 1984), the spread of disturbance (Franklin and Forman 1987, Romme and Knight 1982, Turner 1987, Turner et al. 1989), or net primary production (Sala et al. 1988). Heterogeneity in the landscape can increase gamma diversity by increasing the number of different habitats available. Excessive levels of heterogeneity, however, can result in the loss of species sensitive to habitat fragmentation. Heterogeneity, therefore, must be considered in the context and scale of a particular process or organism. For example, spatial heterogeneity as measured by variation in the type and phenology of food sources could provide a varied, nutritious diet for bears, but increasing spatial heterogeneity by adding unsuitable habitats, such as roads, would not enhance the bear population. In general, the risk of losing biodiversity and disrupting ecological function is greatly increased when natural patterns of heterogeneity are altered.

Results from numerous studies suggest that threshold of connectivity is important to the dynamics of many ecological processes including spread of disturbances (O'Neill et al. 1992, Turner et al. 1989), utilization of resources (O'Neill et al. 1988), and the movement and dispersal of organisms (Gardner et al. 1989, 1991). Landscape connectivity depends, however, on the ability of organisms or processes to move across the landscape. A plant with wind-dispersed seeds is more likely to colonize a small apparently disconnected cluster of habitats than is a heavyseeded plant that lacks a mechanism for long-range dispersal. Similarly, a river or highway might be a barrier to movement for a mouse, but a bird or deer might regularly cross such obstacles.

Critical thresholds in habitat abundance and connectivity can be identified for many organisms, but the values of these thresholds will differ with both the landscape pattern and the scale at which an organism can use the landscape (Pearson et al., in press). A series of simulation experiments conducted with hierarchically generated landscape patterns suggest that when suitable habitat or resources are abundant (e.g., > 80 percent of the landscape), neither landscape-level heterogeneity nor resource utilization scales are important; however, when suitable habitat is less abundant on a landscape, patterning and resource utilization scales become increasingly important. Simulation results suggest that fine-scale fragmentation of habitat poses a greater risk to landscape connectivity than the same percentage reduction of habitat distributed in a more coarse pattern. These results also suggest that the greatest opportunities for improving land management occur at low or intermediate levels of habitat abundance. It is most difficult to predict the consequences of altered landscape patterns at intermediate levels because of complex interactions between pattern and resource utilization scale.

CONCLUSIONS

The recognition of hierarchical structure in landscapes, the effects of disturbances at different spatial and temporal scales, and the scale-dependent effects of heterogeneity requires new perspectives on land management. The following suggestions, originally geared toward maintaining biodiversity in managed landscapes (Pearson, et al., in press), should be useful for maintaining the integrity of landscapes across multiple spatial and temporal scales:

- View the landscape as a whole and use landscape-level indices to measure pattern at multiple scales. Do not focus solely on single, simple concepts like patches and corridors, and recognize that these concepts are scale-dependent.
- Match exploitative or disruptive activities to the natural patterns of heterogeneity. Do not disrupt natural processes such as fire or flooding that create and maintain heterogeneity. Attempt to maintain natural levels of heterogeneity in space and time.
- Maintain connectivity in the landscape by keeping the amount of native habitat in a landscape above potential thresholds of connectivity or by imposing coarse-scale structure on the landscape, or both.

- Be aware of the potential importance of crossing a critical threshold. Small changes in habitat abundance and pattern can suddenly fragment an otherwise well-connected landscape at some (but not all) resource utilization scales. Similarly, small changes in the spatial or temporal scale of disturbance or recovery dynamics can qualitatively change the overall stability of a landscape.

Coarse-grained patterning may have a less deleterious effect on organisms than fine-grained patterning because habitat connectivity can be maintained with less habitat if the habitat has more continuous acreage.

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