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Source: *BioScience*, Vol. 45, Supplement: Science and Biodiversity Policy (1995), pp. S29-S35
Published by: University of California Press on behalf of the American Institute of Biological Sciences
Stable URL: http://www.jstor.org/stable/1312440
Accessed: 06/08/2011 00:57

Ecological Dynamics at Broad Scales

Ecosystems and landscapes

Monica G. Turner, Robert H. Gardner, and Robert V. O'Neill

In response to environmental problems, such as global climate change, land-use change, habitat fragmentation, and loss of biodiversity, ecologists are expanding the scope and scale of their inquiry. The landscape has emerged as a new and exciting level of ecological study (e.g., Forman and Godron 1986, Risser et al. 1983, Turner 1989). Concurrently, emerging paradigms of ecosystem sustainability (e.g., Lubchenco et al. 1991) and ecosystem management (e.g., Agee and Johnson 1988, Slocombe 1993) have encouraged researchers to pursue an understanding of ecological dynamics across broad scales. In addition, the widespread availability of remote sensing imagery, geographic information systems, and high-power desktop computing now permits sophisticated spatial analyses. Indeed, spatial dynamics are considered one of the frontiers of ecology (Kareiva 1994, Levin 1992). Current trends in research and land management suggest that the broad-scale focus in ecology is likely to remain prominent for some time. In this article, we review issues associated with biodiversity at broad scales and suggest some important research needs.

Ecosystem studies have provided a wealth of information about watershed dynamics, energy flow, nutrient cycling, and the importance of different species in maintaining the stability and resilience of natural and managed systems. Studies at long-term research sites, such as Hubbard Brook in New Hampshire, Coweeta in North Carolina, H. J. Andrews in Oregon, and Walker Branch Watershed in Tennessee, have vastly improved knowledge of how ecosystems function. However, the focus on what is considered the whole system has resulted in the dynamics of the parts (i.e., species abundance and diversity) being excluded from the domain of ecosystem science.

We can consider biodiversity in the context of landscape to link population dynamics and ecosystem processes

Now, ability to consider biodiversity in the context of landscape provides enhanced opportunities to link population dynamics and ecosystem processes. Indeed, the traditional paradigm of ecological organization (Figure 1) appears to be insufficient when ecological dynamics are addressed at broad scales or in a spatial context. Therefore, we suggest that an alternative paradigm must be developed.

What do we know?

Pattern-process interactions involving organisms are scale-dependent and require an organism-based view. The appropriate scale (whether spatial or temporal) for evaluating the relationship of an organism or population to its environment varies with the type of organism; for example, a beetle does not relate to its environment on the same scale as does a vulture, even though both are scavengers (Wiens 1989). The studies by Wiens (1976, 1989) have illustrated that different organisms perceive environmental heterogeneity at different scales and that conclusions drawn at one scale may not be applicable at other scales. For example, simply identifying patchiness in an environment does not mean that patchiness is important for a particular species or process. Addicott et al. (1987) have suggested that ecological neighborhoods be defined for organisms by first specifying a particular process (e.g., foraging or reproduction), then identifying the time scale appropriate to the process, and finally addressing the organism's activity or influence during that period.

Two examples, one empirical and one theoretical, illustrate these points. In the empirical example, vegetation classes in study areas on the Oak Ridge Reservation (Tennessee) were mapped as part of a study of habitat use by wintering birds.[1] Vegetation classes included short weeds/grass, fescue, *Andropogon*, tall weeds, short brambles, tall brambles, trees, and saplings. S. M. Pearson[2] then determined by ca-

[1]S. M. Pearson, 1994, unpublished data. Mars Hill College, Mars Hill, NC.
[2]See footnote 1.

nonical correlation analysis that only tall brambles were important for predicting the presence and abundance of five bird species (Carolina wren, *Thryothorus ludovicianus*; northen cardinal, *Cardinalis cardinalis*, rufous-sided towhee, *Piplio erythropthalmus*; song sarrow, *Melospiza melodia*; and white-throated sparrow, *Zonotrichia leucrophrys*). Thus, the initial vegetation classes were modified to predict habitat-use patterns for these bird species. Other species required different maps.

Theoretical studies also illustrate the importance of both the scale at which organisms use the landscape and the abundance and spatial arrangement of suitable habitat across the landscape (Gardner et al. 1992, Pearson et al. in press a). In our theoretical example, three simple rules describe how species can move across a gridded landscape (Figure 2). First, a species' movements may be restricted to the four adjacent grid cells. Second, a species may move to both the adjacent and diagonal grid cells, potentially reaching a total of eight surrounding cells. Third, a species may cross small areas of unsuitable habitat, so a gap the width of one cell does not interrupt a patch. If suitable habitat is randomly distributed across approximately 30% of a landscape, the first species perceives a landscape of small fragmented patches. The second species perceives the landscape as containing somewhat larger patches. The third species perceives a landscape in which suitable habitat occurs in large contiguous patches. Thus, the same landscape is perceived differently depending on what is suitable habitat for a species and the scale at which the species perceives heterogeneity. Clearly, connectivity is a function of both the abundance and spatial patterning of habitat and the organism's scale of resource use (O'Neill et al. 1988, Pearson et al. in press a).

Organisms are influenced by spatial pattern. The influence of spatial pattern on organisms has been well illustrated in numerous studies (e.g., Danielson 1991, Fahrig and Merriam 1985, Hardt and Forman 1989, Milne et al. 1989, Pulliam et al. 1992, and others) and reviews (Kareiva 1990, Wiens 1976). The spatial arrangement—not simply the variance—of resources, habitat, and barriers affects the location, movement patterns, foraging dynamics, and persistence of organisms.

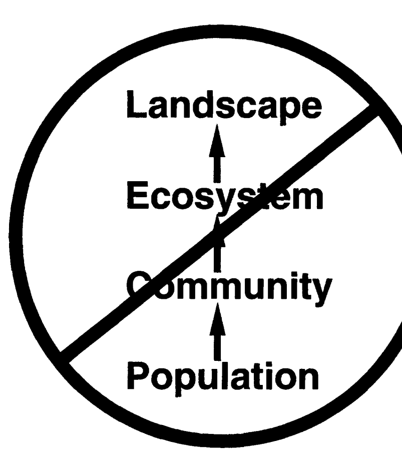

Figure 1. The traditional presentation of levels of ecological organization may not be sufficient to permit understanding of biodiversity issues at broad spatial and temporal scales.

For example, in a study of the effects of fire on the wintering dynamics of large ungulates in Yellowstone National Park, Wyoming, Turner et al. (1994a) demonstrated that a single large fire did not always have the same effect on winter survival of elk (*Cervus elaphus*) and bison (*Bison bison*) as a set of smaller fires, even when the total area burned was the same. Under average to severe winter conditions, survival during the first winter following the fire was greater with the clumped burn pattern than with a fragmented pattern. However, during a mild winter when resources were not limiting, the spatial pattern of fire did not make a difference in elk and bison survival.

Information at broad scales may influence local population dynamics. The dynamics of a local population may be influenced not only by the characteristics of the immediate environment but also by the surrounding landscape. In a study of wintering birds in right-of-way corridors in the Georgia Piedmont, Pearson (1993) quantified habitat characteristics within right-of-way study sites and described the surrounding landscapes by interpreting aerial photography. Stepwise regression analysis revealed that the surrounding matrix explained as much as 74% of the variance in abundance for certain birds (e.g., Parids and rufous-sided towhee) but explained little or none of the variation for other species (e.g., song sparrow and white-throated sparrow). Pearson concluded that the occupancy of a habitat patch may depend on the characteristics of surrounding patches; occupancy may be enhanced if the patch is surrounded by additional suitable habitat.

In addition, an analysis of winter-grazing intensity of ungulates in Yellowstone (Figure 3) also showed that the cumulative winter-grazing intensity on any given hectare of winter range was better explained by broad-scale environmental variation than by the characteristics of that hectare (Pearson et al. in press b). Thus, the landscape context must be considered along with site-specific attributes when describing species abundance and biodiversity (Franklin 1993).

Natural disturbances, by affecting pattern, can be important for biodiversity. Natural disturbances, such as fires, hurricanes, floods, and windstorms, are among the most important generators of pattern in the landscape. Because they are so significant in shaping the environment, because they affect organisms directly, and because they set the stage for future biotic interactions, natural disturbances may have tremendous implications for biodiversity.

For example, during the last three centuries in the area including Yellowstone National Park, large, infrequent fires create the vegetation mosaic that dominates the landscape (Figure 4). A mosaic of burned and unburned forest was observed after the fires of 1988 (Christensen et al. 1989, Turner et al. 1994b), and large, infrequent fires (perhaps occurring only every few centuries) have accounted for most of the total area burned in this landscape in the past several centuries (Johnson and Fryer 1987, Romme and Despain 1989). Fire-history reconstructions suggest that fires of scale comparable to the 1988 fires burned during the early 1700s (Romme and Despain 1989).

The importance of this mosaic for postfire plant reestablishment is becoming clear. For example, the greatest densities of seedlings of the dominant tree species, lodgepole pine (*Pinus contorta* var. *latifolia*), were in areas affected by severe surface fires (i.e., the canopy trees were killed but the needles and cones of the trees were not consumed[3]; Anderson and Romme 1991, Tinker et al. 1994). In addition, lodgepole pine seedling density was negatively related to distance from the nearest severe surface burn, suggesting that boundary shape has an important effect on postfire plant reestablishment.[4]

Disturbance dynamics play an important role in determining community structure—and hence biodiversity. Therefore, it is important to consider changes in disturbance regimes. Such changes might be induced by climatic change, human management, or land-use change. For example, in Yellowstone under a warmer, drier climate, fire frequency would increase, but fire size would decrease. Under a cooler, wetter climate, fire frequency would decrease, but the risk of large fires would increase (Gardner et al. in press). Obviously, such changes in the historic disturbance regime could have considerable implications for biodiversity.

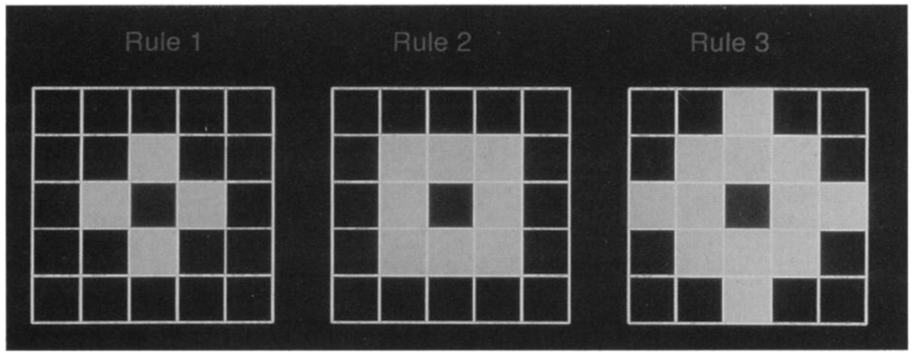

Figure 2. Diagram illustrating three alternative rules by which spatial patterns of habitat might be quantified for species of differing mobility. In rule 1, the species can move only to the four nearest adjacent cells. In rule 2, the species can move to the adjacent and diagonal neighboring cells. In rule 3, the species can jump over a cell of unsuitable habitat.

Populations or guilds have important feedbacks to ecosystem processes and landscape patterns. Organisms influence their environment in a variety of different ways. For example, foraging strategies (e.g., burrowing) may physically alter animals' habitats and influence their community structure and dynamics (Naiman 1988). Soils, sediments, and nutrient dynamics may be affected, which in turn feed back to community structure and the animal population.

The influence of large mammals on ecosystem nutrient dynamics has been well established (e.g., Brown 1984, McNaughton 1985, McNaughton et al. 1988, Seagle and McNaughton 1992). More recently, John Pastor, Yosef Cohen, and Ron Moen have attempted to integrate the foraging strategies of moose (*Alces alces*) with ecosystem processes and the distribution of tree species at the landscape scale.[5] Studies of 40-year-old exclosures on Isle Royale, Michigan, demonstrated that selective foraging by moose on hardwoods results in the increased dominance of spruce, which in turn decreases soil nitrogen availability and microbial activity because the conifer litter is of lower quality than hardwood litter (McInnes et al. 1992, Pastor et al. 1988, 1993). Spatially explicit simulation models have also illustrated that browsing by individual moose imposes structure on initially random landscapes and that the structure varies with the foraging strategy.[6]

Human influences may be dominant factors controlling ecological dynamics at broad scales. Humans continue to alter landscapes at unprecedented rates, and social and economic considerations have become critically important drivers of landscape change. The resulting losses and alterations in habitat are among the primary causes of declines in biodiversity. Therefore, a broad-based understanding of landscape structure and function is essential for promoting an integrated ecosystem-management strategy where human sustenance and environmental integrity are considered equally important goals within the same system (Lee et al. 1992).

The most important factors with respect to the biology of individual species, or even whole communities, may be anthropogenic. In a study of land-use change in Rondonia, Brazil, where tropical rain forest has been cleared rapidly during the past decade, Dale et al. (1994) explored the biodiversity implications of alternative scenarios for agricultural development. These researchers demonstrated that land-use and land-cover changes were a function of sizes and shapes of individual land parcels, attributes of landowners (e.g., residence time), site characteristics such as soils and agricultural suitability, and distances to roads. Worst-case, typical, and best-case development scenarios were simulated spatially, and availability of suitable habitat for a variety of species was evaluated as the landscape changed over time. Species with moderate area requirements and moderate gap-crossing abilities were able to survive under the best-case scenario but were lost within 15 years under the typical scenario. However, species with large area requirements and a limited ability to cross gaps were extirpated within ten years under all scenarios (Dale et al. 1994).

[3]M. G. Turner, W. H. Romme, R. H. Gardner, and W. W. Hargrove, 1995, submitted manuscript. University of Wisconsin, Madison, WI.

[4]See footnote 3.

[5]J. Pastor, Y. Cohen, and R. Moen, 1994, personal communication. Natural Resources Research Institute, Duluth, MN.

[6]J. Pastor, 1994, personal communication. Natural Resources Research Institute, Duluth, MN.

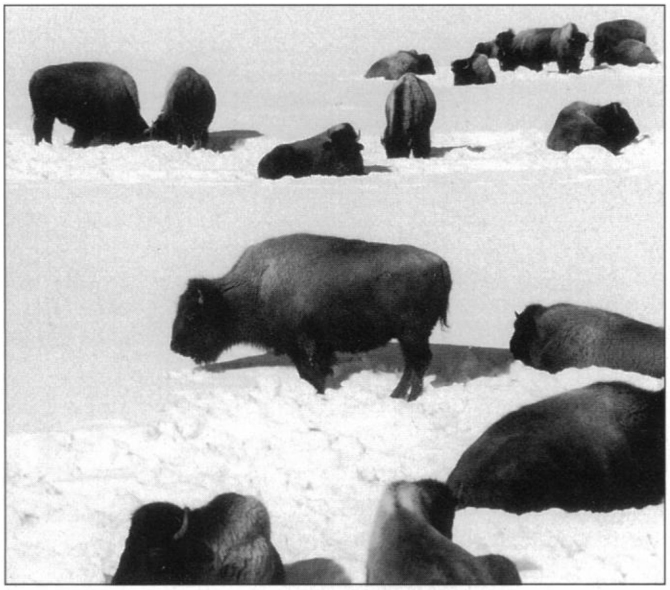

Figure 3. Winter foraging patterns of large ungulates such as bison (top) and elk in Yellowstone National Park, Wyoming, are strongly influenced by the environmental heterogeneity of the surrounding landscape. Broad-scale patterns (bottom) may influence the dynamics of local populations of plants and animals.

In another example, an interdisciplinary study of land-cover change in the Southern Appalachians in western North Carolina and Olympic Peninsula, Washington (Lee et al. 1992), emphasized the links between socioeconomic and environmental drivers of landscape change. It also highlighted the ecological implications of such changes. As part of this study, Turner et al.[7] found that independent variables (slope, elevation, distance to roads, distance to markets, and population density) varied in importance in explaining land-cover change as a function of land ownership. For example, on private lands in the Southern Appalachians, land-cover changes were associated primarily with lower elevations, gentle slopes, and closer proximity to roads and developed areas. These factors were not associated with land-cover changes on public lands. Thus, social and economic variables—not only biophysical ones—need to be understood in predicting landscape change.

[7]M. G. Turner, D. N. Wear, and R. O. Flamm, 1994, submitted manuscript. University of Wisconsin, Madison, WI.

What do we need to know?

The development of scientifically sound policies for maintaining species abundance and biodiversity is likely to require an understanding of the effects of landscape and ecosystem change on populations and communities. We suggest six areas that represent policy-relevant research needs.

Describing organism-process interactions, especially feedbacks in spatial terms. There is a large body of literature describing the effects of spatial pattern on the presence or abundance of populations. However, there is little research on the relationship between the species dynamics and ecosystem processes in a spatial context. In addition, the potential feedback effects of the populations on ecosystem and landscape dynamics are poorly understood.

Better integrating population ecology and landscape ecology. Traditional distinctions between ecological subdisciplines may limit our understanding of biodiversity at broad scales. Better integration is needed. For example, metapopulation dynamics have been emphasized in both population and landscape ecology studies, but there is much to be gained from enhanced communication and collaborative studies. Foraging theory is another example of a large body of knowledge that might be applicable at broad spatial scales and in which explicit spatial dynamics may be better addressed.

Understanding and predicting when spatial pattern matters. Currently, the ability to quantify spatial pattern and monitor changes in pattern exceeds the ability to interpret its ecological effects. Furthermore, quantitative measures of landscape pattern in land management are being increasingly used, but with insufficient attention paid to their intrinsic assumptions and constraints. Determining what constitutes a significant change—both statistically and ecologically—in spatial metrics, and relating such changes to ecologically relevant responses, remain critically important research tasks.

Developing a library of empirical studies of pattern-process interactions. Requisite to an understanding of when pattern matters is the development of a literature of empirical studies that demonstrate particular relationships between spatial pattern and ecological processes. In addition to the studies currently in progress (and their numbers may be increasing gradually), ecologists need to compare the effects of pattern on the same process in different locations and at different spatial and temporal scales and compare the effects of the same pattern on different processes. Broad-scale empirical studies may require the development of hypotheses that can be tested by comparison. Creativity in approach remains crucial.

Identifying the controls on ecological processes at different spatial and temporal scales. The factors that control ecological processes at fine scales may be quite different from those operating at broad scales. Both theoretical and empirical studies must address multiple scales, and a hierarchical understanding of the mechanisms and controls is sorely needed. For example, the persistence of a population within a single habitat patch may depend on the species' ability to locate food and avoid predation within that patch. The persistence of the population in the landscape, however, may depend on the vagility of the species and the abundance and spatial arrangement of suitable patches. Without an understanding of scale-dependent changes in controlling factors, ability to manage biodiversity at landscape or regional scales is likely to remain limited.

Integrating socioeconomic and ecological dynamics. Although natural ecological systems pose many interesting research questions, there is a crucial need for a better understanding of the human drivers of ecological change. Such an understanding requires interdisciplinary approaches and the inclusion of independent variables that often are excluded from ecological studies (e.g., population density, interest rates, road networks, and commodity prices) but that may in fact be driving changes in ecological response variables (e.g., biodiversity).

Figure 4. Vegetation reestablishment in the subalpine forests in Yellowstone National Park was strongly influenced by the spatial mosaic of burn severities created by the large fires of 1988.

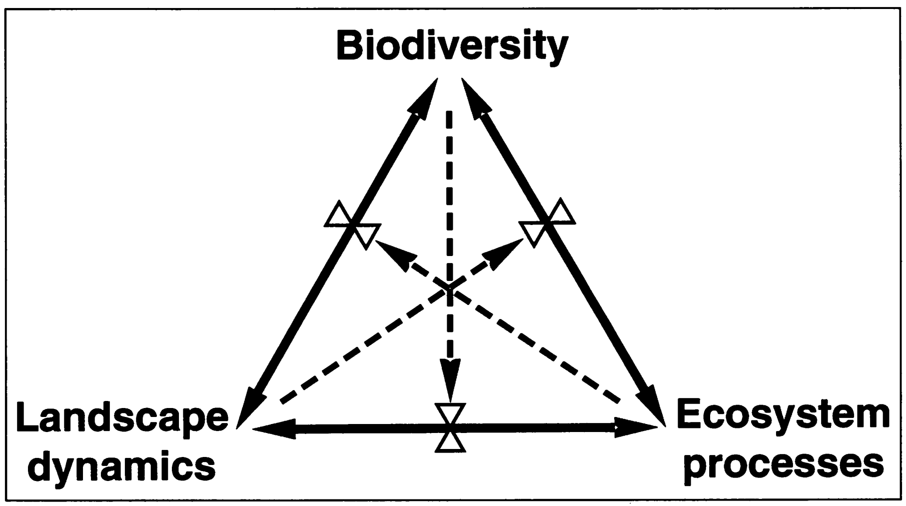

Figure 5. An alternative approach for considering ecological interactions at broad scales. We suggest that understanding these relationships and the controls operating on them at multiple scales is a crucial challenge for ecology. Dashed arrows indicate influence. Solid lines indicate direct interactions. Hourglasses indicate controls.

Challenges to broad-scale ecological studies

It is important to recognize two major challenges to broad-scale ecological studies. First, assembling spatial databases over large areas—building the geographic information system databases needed for analysis and modeling—is time- and cost-intensive. This activity requires a large initial investment, and researchers frequently underestimate both the time and money required.

Second, broad-scale experimentation is often logistically impossible. Alternative approaches to the traditional experiment must be used more often and more creatively, and existing technologies, such as remote sensing and geographic information systems, must be better integrated. A variety of approaches to broad-scale studies can be used to advantage. Existing land-management activities can be studied, as is well illustrated in studies of forest-cutting patterns (e.g., Franklin and Forman 1987). Study areas can also be selected to make use of existing differences or gradients in a parameter of interest. For example, sites arrayed along a land-use gradient or areas with different amounts or arrangements of habitat could be studied. Large-scale natural events, such as fires, floods, or storms, can also be studied from an experimental viewpoint. Small heterogeneous areas that may serve as analogues for larger landscapes can be manipulated under direct experimenter control, although issues associated with extrapolation across scales must be addressed.

The need for a new paradigm

The ecological organization taught in introductory ecology classes (Figure 1) is not sufficient to yield an understanding of ecological dynamics at broad scales. When considering landscape or regional ecological dynamics, the population can no longer be considered to be subsumed by the community, which is in turn included within the ecosystem, which is itself included within the landscape. Rather, we suggest an alternative paradigm in which two-way interactions among biodiversity, ecosystem processes, and landscape dynamics are examined with the explicit effects of the third factor (Figure 5). Frequently, the two-way interactions are examined under the assumption that the third factor does not vary or exerts little influence. This assumption simply does not apply when questions are expanded to broad scales.

This alternative paradigm identifies additional research needs. For example, there are many studies of how landscape dynamics influence biodiversity (Figure 5), but the effects of variation in ecosystem processes on this relationship are often not considered. In addition, there are few studies of how biodiversity influences landscape pattern, a potentially important feedback. Similarly, there is detailed knowledge of how some species influence ecosystem processes, but the influence of the landscape and spatial variation of their interactions is poorly understood. Finally, the interactions between landscape dynamics and ecosystem processes are not well understood, and the potential influences of biodiversity on this interaction are even less well known.

We suggest that the challenge to ecologists for the next decade is to address these complex interactions in ways that aid the development of scientifically sound public policy.

Acknowledgments

Funding for this article was provided by the National Science Foundation (BSR-9018381) and the Ecological Research Division, Office of Health and Environmental Research, US Department of Energy, under contract no. DE-AC05-84OR21400 with Martin Marietta Energy Systems Publication No. 4383 of the Environmental Sciences Division, Oak Ridge National Laboratory.

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