



all. At worst, they are analogs of how we imagine nature to work, not how it actually works. At best, the task of assembling, maintaining, and predicting the behavior of even moderately complex ecosystems in the laboratory tests our understanding to the limit (7). More than anything else, model systems act as a bridge between theory and nature (1). They are not a substitute for studying the real thing, but by simplifying the complexities of nature, model systems can sharpen our understanding of natural processes.

The next decade is likely to see a big increase in the use of model laboratory systems in ecology. The trend is toward more complex and more realistic assemblages. The majority of studies to date have built communities from the bottom up, by the introduction of species into an abiotic environment. But an alternative is to move the field, as buckets of water or intact blocks of soil, complete with biota, into a CEF, blurring still further the already fuzzy distinctions between laboratory microcosms, mesocosms maintained outdoors, and field manipulation experiments.

The advantages of model laboratory systems for ecology are replicability, reproducibility, mastery of environmental variables, ease of manipulation, and control over who enters the ark. Because they can involve creatures with short generation times and usually run without seasons, model systems also speed up nature. Claimed disadvantages include their taxonomic and structural simplicity, lack of spatial and temporal heterogeneity, small physical size, and concerns about whether organisms that thrive in microcosms and mesocosms are representative of those that do not. Some of the things that model laboratory systems are not good at are well described by Carpenter *et al.* (9). These criticisms and problems matter if we blindly extrapolate from the laboratory to the field. They do not matter if we treat the problems as research questions (7): What differences do size, simplicity, or lack of seasonality make to ecological processes? And these criticisms are irrelevant if we see model systems as one part of a rich, interrelated web of approaches to understanding and predicting the behavior of populations and ecosystems.

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Landscape Ecology: Spatial Heterogeneity in Ecological Systems

S. T. A. Pickett and M. L. Cadenasso

Many ecological phenomena are sensitive to spatial heterogeneity and fluxes within spatial mosaics. Landscape ecology, which concerns spatial dynamics (including fluxes of organisms, materials, and energy) and the ways in which fluxes are controlled within heterogeneous matrices, has provided new ways to explore aspects of spatial heterogeneity and to discover how spatial pattern controls ecological processes.

Landscape ecology is the study of the reciprocal effects of spatial pattern on ecological processes (1); it promotes the development of models and theories of spatial relations, the collection of new types of data on spatial pattern and dynamics, and the examination of spatial scales rarely addressed in ecology. Throughout much of its history, ecology sought or assumed spatial homogeneity for convenience or simplicity; scales

that lent an apparent uniformity to the processes under study were emphasized, and heterogeneity was taken as a necessary evil or an unwelcome complication. In contrast, landscape ecology regards spatial heterogeneity as a central causal factor in ecological systems, and it considers spatial dynamics and ecology's founding concern with the temporal dynamics of systems to be of equal importance. Factors in temporal dynamics include population growth and regulation, community dynamics or succession, and the dynamics of evolutionary change. The spa-

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tial effects of these factors were not entirely ignored before the advent of landscape ecology; some of the oldest roots of ecology are in biogeography. Similarly, evolutionary biology contributed the concern with population subdivision and the role of spatial segregation in population differentiation and speciation.

Ecology uses the concept of a landscape in two ways. The first, which considers a landscape as a specific area based on human scales, is intuitive: Landscapes are ecological systems that exist at the scale of kilometers and comprise recognizable elements, such as forest patches, fields and hedgerows, human settlements, and natural ecosystems (2). The second use of landscape is as an abstraction representing spatial heterogeneity at any scale. In this guise, the landscape is an ecological criterion (3) for a spatial approach to any ecological system. Irrespective of the landscape concept used, there are two major approaches to landscape ecology, reflecting differences in scale. The most common approach is the elucidation of the interactions among the elements of a matrix, especially adjacent ones. This focus exposes the relatively fine-scale mechanisms behind the dynamics and structure of the entire matrix. The second approach focuses on the coarse-scale dynamics and behaviors of the matrix as a whole. The two approaches are complementary, and both recognize a spatial mosaic with discrete elements. New technologies, such as geographic information systems and electronic databases, integrate these approaches (Fig. 1).

Spatial Mosaics

Although all landscapes can be thought of as mosaics, this concept is most easily exemplified by human-dominated landscapes (Fig. 1). Landscapes are composed of discrete, bounded patches that are differentiated by biotic and abiotic structure or composition. A predominant, continuous patch or cover type acts as a matrix in which other patch types appear. For example, forest patches are embedded in a matrix of farm fields. There are important correlations between patch characteristics and the ecological parameters within them. For instance, experimental forest fragmentation in the Amazon (4) has revealed that the number of carrion beetles declines with forest fragment size, as does bird diversity. The heterogeneity in landscapes can determine animal population response (5), and landscape matrix variables often explain more of the variation in the abundance and diversity of birds than do within-habitat factors (6). How landscapes are structured is a fundamental question in landscape ecology. In an application of graph theory to 25 land-

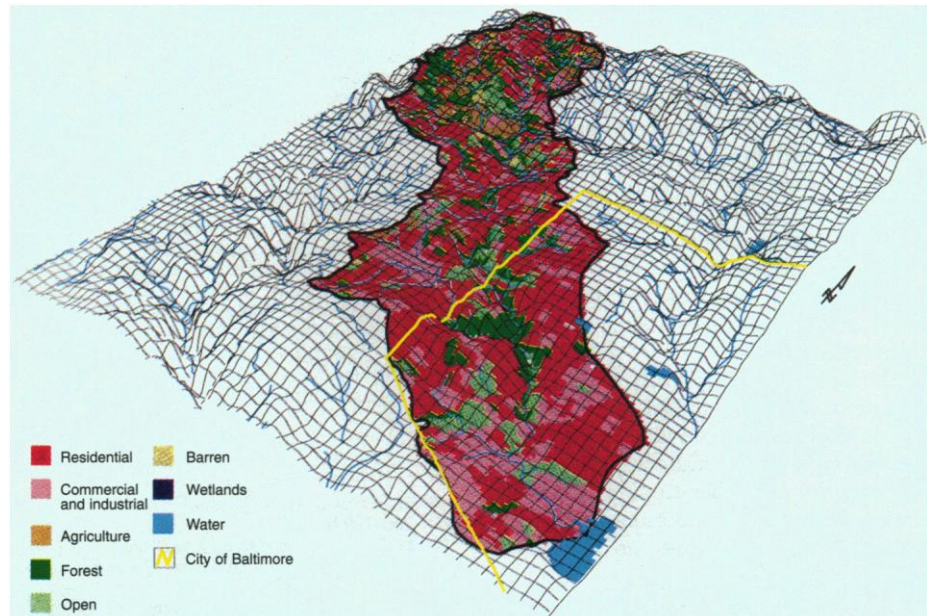


Fig. 1. Landscape of the Gwynns Falls watershed (Baltimore, Maryland) showing patch type, size, and configuration, and illustrating structures such as corridors. Finer resolution would expose specific ecological community types. Research on the reciprocal linkages among social, ecological, and hydrological processes uses the spatial configuration of the landscape as the organizing model. Map courtesy of the Revitalizing Baltimore Program and J. M. Grove.

scapes, in which nodes represented landscape elements identified by aerial photographs and connections between nodes represented contacts between elements (7), 90% of the resulting graphs were "spiders," "necklaces," or loops (Fig. 2). This predominance of a few kinds of patterns in different human-dominated landscapes suggests regularities in underlying ecological processes. The patterns suggest comparison with other spatial scales and with landscapes less impacted by humans.

The origins of structure in mosaics are diverse. Patches can arise because of natural or human-caused disturbance, fragmentation of a land cover type, regeneration of a type, persistent differences in environmental resources, or introduction by humans (2). Purely biotic causes of patch formation include the accidents and spatial localization of dispersal of seeds or young, and the spatial segregation resulting from interactions between competitors or between predators and prey. Many such agents of patch formation are episodic. Therefore, patches may form at different times and places in landscapes, leading to a shifting mosaic. After patch formation, environmental conditions or relations among organisms in the patch may change through time. Taken together, the spatial pattern of patch creation and the changes within patches constitute patch dynamics. An example of patch dynamics emerges from the 1988 fires in Yellowstone National Park, which influenced not only patch formation and location but also the subsequent community

changes within patches and the response of grazing animals to that shifting mosaic. The disturbance patches in Yellowstone are so large that the mixture of patch types is not at equilibrium over the long term (8). In contrast, disturbances that recur at short time intervals or finer spatial scales can produce an equilibrium patch distribution in a landscape (9). Spatial pattern also exists in marine, freshwater, and wetland environments (10); thus the term "landscape" is not restricted to terrestrial environments.

Landscape pattern can also exist at much finer scales than the examples above. The activities of animals, such as digging and burrowing, can generate spatial heterogeneity (11). Additional examples of fine-scale heterogeneity include the contrasting surface types in deserts, such as rock versus soil or bare soil versus shrub-covered patches (12). Thus, landscape heterogeneity can be expressed at scales that are within the spatial scope of most ecosystem types recognized by ecologists and resource managers.

Flux in Landscapes

Understanding how neighboring elements affect one another, or how they affect a process, is quite different from classical ecological concerns with the structure and function of discrete communities, populations, or ecosystems (13). One of the most well-studied aspects of landscapes is the role of edges (14), such as those of forests. Seed or animal dispersal from forests into fields or

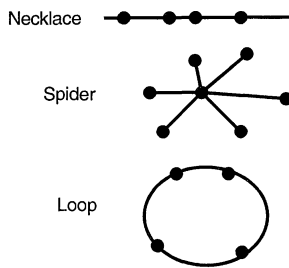


Fig. 2. Graph types revealed by analysis of aerial photographs of 25 landscapes (7). Necklaces, spiders, and graph cells or loops were the most common types of connections abstracted.

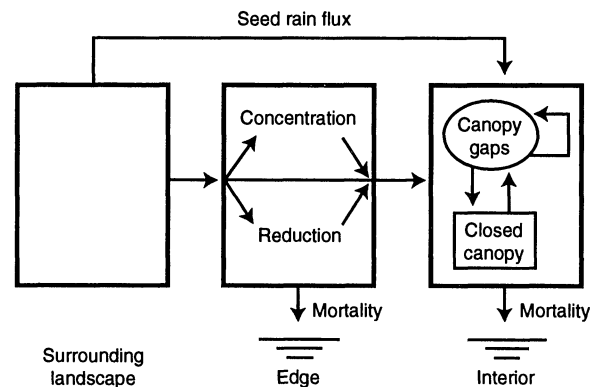
clear-cut areas is a widely documented effect on landscape organization. Even the seed stored in some forest soils reflects the current dispersal into the forest more closely than it reflects the identity of the prior occupants of the site (15).

The effects of the forest exterior on processes in the interior are a common topic of concern in landscape ecology. In agricultural landscapes, predation on nests of forest interior birds often decreases with distance from the forest edge (16). The edges of newly isolated tropical wet forest patches experience greater tree mortality and increased recruitment of pioneer species (4). However, simplistic and static views of how edges function can limit understanding of how landscape spatial structure works (17). How these fluxes are actually mediated by the edge is an open question (18) that is beginning to be experimentally examined. Edges can facilitate, inhibit, or remain neutral to crucial fluxes across them as a result of alterations in such mechanisms as wind and water flows, physical limiting factors, habitat availability, animal disperser availability or activity, competition, herbivory, and predation (Fig. 3).

Mosaic structures can have a major influence on fluxes of organisms and materials. For example, the species richness and abundance of cavity-nesting birds were associated with patch orientation relative to their migration path but were not affected by patch shape, whereas resident species did not respond to landscape configuration (6). Landscape configuration also affects biogeochemical fluxes. The flux of CO_2 (19), and the movement of various forms of N (20), for example, are determined on the landscape scale by human land uses.

Gene flow and population differentiation are well known to respond to spatial heterogeneity (21). However, the specific ecological processes that link these population factors to their specific landscapes must be determined (22). The concept of a meta-population—a population that is spatially subdivided yet connected by dispersal—originated in population genetics

Fig. 3. A conceptual model illustrating the possible net effects of the edge of a landscape element on flows from the exterior to the interior of the element. With plants as the motivating organism, the model suggests that the flux from the surrounding landscape is mediated in the edge by concentration (for example, by establishment of seeds and subsequent reproduction of adults) or reduction (for example, by predation of dispersing seeds). Alternatively, the edge may have no net effect, or the flux may avoid the edge, as in dispersal into canopy gaps.



but has strong links to the landscape approach (23). Theory assumes that populations of a species occur as isolated patches, and that extinction of populations is compensated for by establishment of populations in other patches. The approach has proven valuable in understanding population extinction, establishment, and abundance (24). Various models indicate that coexistence can result from many specific mechanisms, notably differences in dispersal rates and spatial aggregation of superior competitors (25).

Landscapes and Scale

Landscape ecology is concerned with the causes and effects of heterogeneity rather than with a specific range of spatial scales. However, the degree to which heterogeneity is expressed depends on scale. The basic question about scale in ecology consists of determining whether a given phenomenon appears or applies across a broad range of scales, or whether it is limited to a narrow range of scales (26). Therefore, the search for breaks in scale and the discovery of scales appropriate to different ecological phenomena are critical.

The distribution limits of species of *Quercus* from the arid U.S. southwest constitute an example of how a phenomenon in a landscape is caused by processes that occur at different scales. Seedling establishment is controlled by an interaction of local and regional precipitation, whereas mortality is determined by local elevational changes in moisture relations and the degree of openness of the canopy (27). A second example uses scale to explain patterns of animal body size in contrasting ecosystems. Holling (28) used hierarchical landscape structure as a tool to expose structure in the body size distributions of animals and to link community characteristics with ecosystem productivity. The utility of the approach in contrasting biomes suggests that landscapes can act as a unifying concept in diverse environments.

Humans as Components of Landscapes

Although humans are a conspicuous element of landscapes at the coarse scale, ecologists have struggled to study ecological entities devoid of human influence. However, studies of superficially human-free systems can yield misleading results because the structure and function of systems often reflect human influences that are not obvious (29). There are very few landscapes that do not bear the contemporary, or historical but persistent, stamp of humankind. Landscape ecology has stimulated ecologists to study humans (2) and to interact with other disciplines that are concerned with humans as individuals, societies, and institutions (30).

Human influences on landscapes include altered disturbance types and patterns, addition of new or chronic pollution stresses, widespread alteration of atmospheric chemistry, and introduction of exotic organisms. The spatial extent of these influences is increasing (31); not even apparently remote ecosystems have entirely escaped them. Other large human influences, such as the effects of preindustrial land use on species composition, are subtly hidden in the past. However, ecologists are becoming more knowledgeable about such effects and are incorporating human activities into their concepts and models. Not only does this step enhance basic ecological understanding, it places ecologists in a better position to inform conservation, restoration, and management efforts.

Conclusions

Landscape ecology is a relatively new specialty, which—like all of ecology—is integrative. It consolidates the understanding of the nature, causes, and effects of spatial heterogeneity that ecology had accomplished over many decades. Although that is a useful synthesis in itself, landscape ecol-

ogy has produced some additional insights. Primary among these is the knowledge that the spatial heterogeneity in ecological systems at various scales often influences important functions, ranging from population structure through community composition to ecosystem processes, and that traditional within-patch explanations were incomplete. Landscape ecology has begun to determine the mechanisms behind the relations of spatial pattern and ecological processes. The heterogeneity of entire matrices as well as the structures of specific boundaries in landscapes have been shown to govern the movement of organisms, materials, and energy. Landscape ecology has become a major stimulus for clarifying the fundamental problem of scale in ecology by showing how processes at various scales interact to shape ecological phenomena and by exposing regularities that have wide explanatory potential. Finally, landscape ecology has focused the attention of ecologists on scales and systems in which human impacts, even subtle and distant ones, are necessary ingredients in ecological models. Together, these advances have brought spatial heterogeneity into ecology to perform valuable explanatory and predictive functions, rather than excluding it as a troublesome source of error.

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Ecology and Climate: Research Strategies and Implications

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Natural and anthropogenic global changes are associated with substantial ecological disturbances. Multiscale interconnections among disciplines studying the biotic and abiotic effects of such disturbances are needed. Three research paradigms traditionally have been used and are reviewed here: scale-up, scale-down, and scale-up with embedded scale-down components. None of these approaches by themselves can provide the most reliable ecological assessments. A fourth research paradigm, called strategic cyclical scaling (SCS), is relatively more effective. SCS involves continuous cycling between large- and small-scale studies, thereby offering improved understanding of the behavior of complex environmental systems and allowing more reliable forecast capabilities for analyzing the ecological consequences of global changes.

As they increase in numbers, humans are using technology to achieve higher standards of living (1). As a consequence, we continue to modify atmospheric composition, water quality, and land surfaces, as well as introduce a host of novel chemicals into the environment. In addition, we have transported species beyond their natural boundaries, creating exotic invasions (2). When such changes occur on a global scale (for example, climate change caused by an enhanced greenhouse effect), or regionally but with sufficient frequency as to be global in scope (for example, habitat fragmentations), they are defined as “global changes.” The potential severity of these changes has motivated substantial efforts to understand their ecological implications (3–9).

The ecological implications of any global change are difficult to predict for several reasons. First, the rates of human-induced change are often an order of magnitude faster than those related to natural causes, which limits the reliable application of historic analogs (10–12). Second, the scales at which different research disciplines operate [climate modelers typically use grid squares

500 by 500 km (13), whereas ecologists primarily use tennis-court-sized field plots (14)] make interdisciplinary connections difficult and necessitate devising methods for bridging scale gaps (15, 16). Third, many disciplines must be integrated. Fourth, uncertainties exist in virtually every aspect of the analyses [for example, baseline data (17, 18)]. Furthermore, actions to mitigate potential ecological implications are controversial, because policy options often involve substantial investments that, even if macroeconomically efficient, may dramatically alter regional economic, social, or demographic status quos (19, 20), and because diverse audiences require education about uncertainties and potential risks.

The urgency of global change issues demands bold attempts to overcome these obstacles. From a public policy perspective, more reliable predictive power could help society mitigate potential impacts by reducing the factors that force global changes (21) [for instance, reducing greenhouse gas emissions through fees on carbon releases (22)]. In addition, investigation of possible ecological responses may indicate how humans could facilitate the adaptation of managed and unmanaged ecosystems to global changes (23), thereby minimizing plausible damages and maximizing potential opportunities. Examples of such “insurance policies” include accelerating development of less-polluting energy systems (24) and

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