

Landscape Ecology

A hierarchical perspective can help scientists understand spatial patterns

Dean L. Urban, Robert V. O'Neill, and Herman H. Shugart, Jr.

A terrestrial landscape is a mosaic of heterogeneous land forms, vegetation types, and land uses. The study of landscape—its spatial patterns and how they develop—is presently emerging as a new discipline in the field of ecology (Forman 1981, 1983, Forman and Godron 1981, 1986, Naveh and Lieberman 1984, Noss 1983, Risser et al. 1984). Landscape ecology is motivated by a need to understand the development and dynamics of pattern in ecological phenomena (Clark et al. 1978, Levin 1976a,b, 1978, Whittaker and Levin 1977, Wiens 1976), the role of disturbance in ecosystems (Mooney and Godron 1983, Pickett and White 1985, Sousa 1984, White 1979), and characteristic spatial and temporal scales of ecological events (Allen and Starr 1982, O'Neill et al. 1986).

Pattern, generated by processes at various scales, is the hallmark of a landscape. In this paper we outline an approach to landscape study that employs a hierarchical paradigm of pattern and behavior. Although our em-

Dean L. Urban is a research associate and Herman H. Shugart, Jr. is the Corcoran Professor of Environmental Sciences in the Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903. Robert V. O'Neill is a senior research ecologist in the Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831. They study the development and dynamics of scaled pattern in ecosystems. © 1987 American Institute of Biological Sciences.

A landscape is a mosaic of patches, the components of pattern

phasis is on forested landscapes, we can generalize a theory of landscape ecology.

Landscape pattern and process

We will first focus on the wide range of phenomena in a natural terrestrial landscape by considering the apparent complexity of landscape dynamics and illustrating how a hierarchical paradigm lends itself to simplifying such complexity. Our perspective also affords insights into the management of man-dominated landscapes.

Development of landscape pattern. A landscape is a mosaic of patches, the components of pattern. The agents of pattern formation on natural landscapes can be categorized as disturbances, biotic processes (especially the demographic processes of birth, death, and dispersal), and environmental constraints (Levin 1978). Each of these agents can be considered across a spectrum of spatial and temporal scales. For example, disturbances that affect terrestrial landscapes vary in spatial extent, recurrence interval, and intensity (Pickett and White 1985, Sousa 1984, White 1979). Disturbances range from the localized effects of an individual

death to the large-scale effects of wildfires, drought, and epidemic disease. Biotic, or regenerative, processes also vary in scale from the regrowth of an individual to the reorganization of species assemblages. Environmental constraints include microclimatic and fine-scale soil conditions governing seed germination, and also sub-continental climatic regimes that delineate biomes, such as the Eastern Deciduous Forest.

The agents of pattern formation are interwoven in landscape development. This interaction allows some sites to be especially prone to, or sheltered from, disturbances. For example, topographic position interacts with fire frequency; dry ridges burn more frequently than moist (mesic) coves. Regenerative processes are influenced by site quality, and also vary with the age and life-history attributes of the regenerating individuals (Odum 1969, Shugart and Hett 1973). Moreover, both disturbances and regeneration may be constrained by the existing spatial pattern (Curtis 1956, Forman 1981, Watt 1947). Finally, new patches are continually superimposed on existing patches (Reiners and Lang 1979). The emergent scenario is a mosaic of patches of various size, of various origins, in various stages of regeneration, approaching microenvironmental equilibria at various rates. Such complexity would seem overwhelming at first and any attempt to fully understand landscapes would appear futile.

Organization of landscape pattern. But importantly, the complexity of

landscape pattern is organized in a special way: the component events and patches occur at characteristic scales that are positively correlated in time and space. Disturbances, for example, occur over a wide range of space and time scales, but those affecting a particular landscape typically can be divided into events occurring on characteristic scales. For example, Romme and Knight (1982) were able to break the fire regime in Yellowstone Park into two components: frequent, small fires (every few decades, affecting areas of less than 100 ha); and larger, less-frequent fires (every few centuries, affecting areas of several hundred ha). Similarly, Heinzelman (1973) documented a two-scale fire regime in the Boundary Wa-

ters Canoe Area of Minnesota. The concept of disturbance is itself implicitly scaled; if disturbances are events that kill trees prematurely, then "disturbance" is confined to a relatively narrow window of time corresponding to the lifespan of trees (Figure 1a). Events outside this domain, while they may affect trees, are not considered disturbances. Small-scale disturbances tend to occur more frequently while larger events tend to be less frequent.

Demographic processes are also scaled. Individuals have characteristic sizes and lifespans that dictate correspondingly scaled patterns (Watt 1947). Species dispersal distances and rates define the scale of larger and longer-term patterns (Figure 1b). At

still larger scales and over longer spans of time, genetic fluxes define the domains of adaptation and evolutionary processes.

Environmental constraints are scaled by the manner in which we witness them. Atmospheric conditions can be observed at virtually any scale, but "microclimate," "weather," and "climate" connote phenomena witnessed over increasingly larger areas and longer timespans. Likewise, we could also measure soil processes at virtually any scale, but we would not measure the chemical weathering of minerals over the entire Canadian Shield (we would use a small, representative surface), nor would we observe the evolution of landforms on a single hillslope (where we would

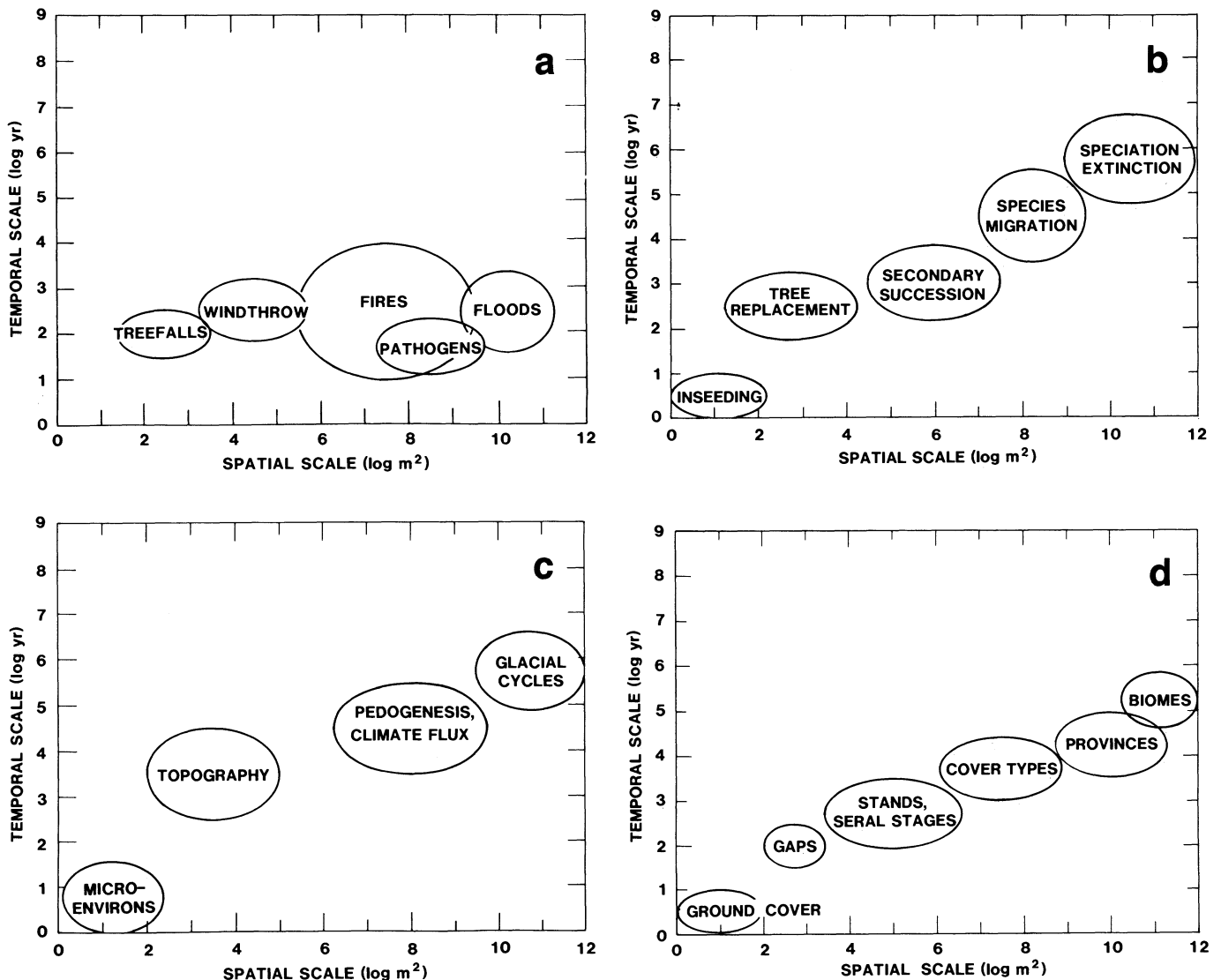


Figure 1. (a) Disturbance regimes, (b) forest processes, (c) environmental constraints, and (d) vegetation patterns, viewed in the context of space-time domains. Modified from Delcourt et al. (1983).

study erosional processes). The phenomena we study tend to be positively correlated in time and space (Figure 1c).

Vegetation patterns can be resolved on different scales (Figure 1d). Whittaker's (1953) notion of climax pattern was a two-level description of vegetation pattern that reconciled the broad-scale idea of a single stable community of plants dictated by climate (Clements 1916) with fine-scale observations of individual plant communities (Gleason 1939). Moreover, the large-scale generalization is only loosely coupled to the fine-scale details of a phenomenon. The successional schemes described by Clements may apply in general to large areas, but they do not predict with certainty what one will actually find on a particular site at a given time. This loosely coupled, multileveled organization of landscapes requires a new conceptual model. We suggest a paradigm that comes from hierarchy theory (Allen and Starr 1982, Allen et al. 1984, O'Neill et al. 1986, Pattee 1973, Whyte et al. 1969).

The paradigm

Hierarchy theory is concerned with systems that have a certain type of organized complexity. Hierarchically organized systems can be divided, or decomposed, into discrete functional components operating at different scales (Simon 1962). As applied to landscape ecology, the hierarchical paradigm provides guidelines for defining the functional components of a system, and defines ways components at different scales are related to one another (e.g., lower-level units interact to generate higher-level behaviors and higher-level units control those at lower levels). This paradigm can aid the design of studies in landscape ecology and the prediction of how external factors will alter an ecosystem.

Natural phenomena often are not perfectly decomposable: spatial boundaries may be difficult to define precisely and components may interact. Yet many complex, natural phenomena are nearly decomposable (Allen and Starr 1982, O'Neill et al. 1986, Simon 1973) and thus can be conceptualized usefully as hierarchical systems.

Hierarchical structure. Components of a hierarchical system are organized into levels according to functional scale (Figure 2). Events at a given level have a characteristic natural frequency and, typically, a corresponding spatial scale. In general, low-level events are comparatively small and fast; higher-level behaviors are larger and slower. More strictly, components of a hierarchical system may be ordered into levels according to a number of criteria (Allen et al. 1984). Higher levels may be larger than, slower than, constrain (control), or contain lower levels. In many of the hierarchies we will consider, all criteria will apply. The rules structuring hierarchies can be conveniently illustrated through an extended example.

Let us develop a hierarchy to study the species-composition dynamics of a deciduous forest system in the eastern United States. The forest gap has long been recognized as a functional unit in forest systems (Watt 1925, 1947; see also Bormann and Likens 1979, Shugart 1984). When a large tree dies, it creates a gap where subordinate trees may thrive under a regime of greater resources now available to them. A transitional stage of

scramble competition ensues, until another tree grows large enough to become dominant. When this tree dies, the cycle repeats. The spatial unit of gap dynamics is equal to the area affected by the death of a canopy-dominant tree; its natural frequency reflects the lifespan of the dominant species (Shugart 1984, Shugart et al. 1981).

Trees within a forest gap interact much more among themselves, by virtue of their shared regime of available resources (especially light), than they do with trees beyond the gap. These interactions define the boundaries of a gap. By extension, a larger forest area can be decomposed into a mosaic of gap-sized patches, in which each gap undergoes its own dynamics. But the gaps are neither identical nor completely independent. The gaps comprising a mesic cove share similar species under similar growing conditions, and they exchange seeds and nutrients more often within the cove than with gaps on a nearby ridge. Again, these similarities allow us to delineate an area of characteristic size within which gaps interact at a characteristic frequency, and allow us to define stands as higher-level compo-

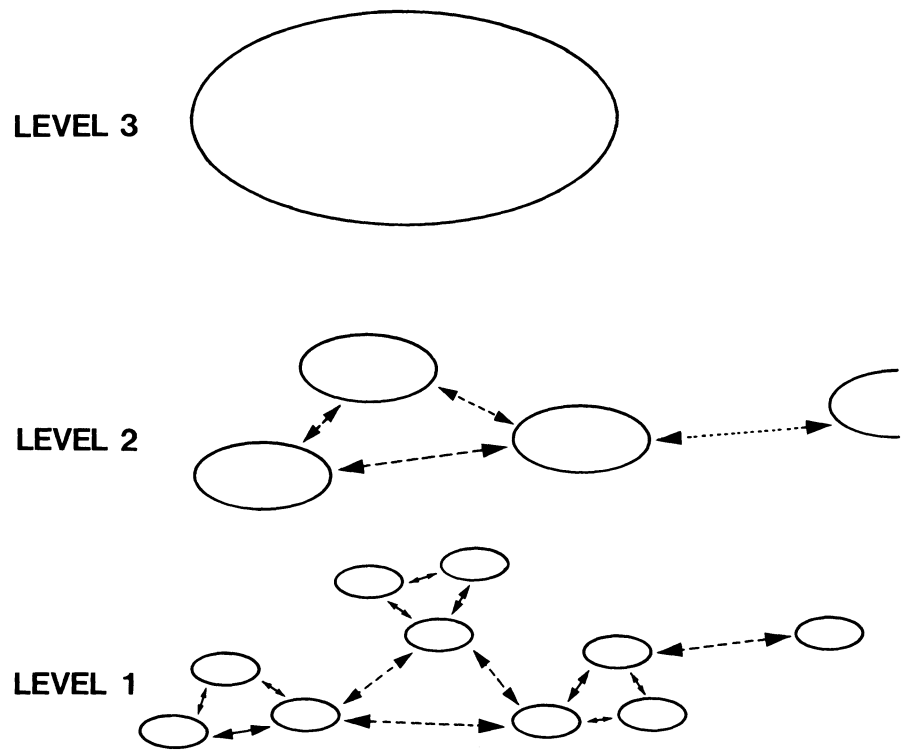


Figure 2. A generalized hierarchical system. Thick arrows indicate strong interactions; broken arrows, weak interactions.

FOUR LEVELS OF A FOREST HIERARCHY

LEVEL	BOUNDARY DEFINITION	SCALE
LANDSCAPE	PHYSIOGRAPHIC PROVINCES; CHANGES IN LAND USE OR DISTURBANCE REGIME	10000s ha
WATERSHED	LOCAL DRAINAGE BASINS; TOPOGRAPHIC DIVIDES	100s–1000s ha
STAND	TOPOGRAPHIC POSITIONS; DISTURBANCES PATCHES	1s–10s ha
GAP	LARGE TREE'S INFLUENCE	0.01–0.1 ha

Figure 3. A forested landscape as a hierarchy of gaps, stands, and watersheds.

nents of a forest hierarchy.

Moving upscale once again, we might define watersheds at the next higher level, because stands within a watershed share a similar resource base and interact more among themselves than they do with stands in other watersheds. At a still higher level, we might define landscapes as units of similar, interacting watersheds. At the landscape scale, boundaries might be coincident with large-scale physiographic features (e.g., mountain ranges) that govern weather patterns and limit frequencies of species movement. Of course, such landscapes interact as well, giving definition to still higher levels, for example, regional forest provinces, such as a spruce-fir forest.

We have constructed a four-level hierarchy to represent a forest (Figure 3). At each level, similar and interacting components become the functional aggregates at the next higher level. This is a rate-structured hierarchy, because components of one aggregate interact more frequently and intensively among themselves than with components of other aggregates. This rule defines the horizontal structure (within levels) as well as the vertical structure (between levels) of a hierarchical system. Interactions among components at one level generate the behaviors of a component at the next higher level. A gap has its own internal dynamics, but it also contributes to the behavior of a stand. In turn, a stand's behaviors are not only its own, but also are a part of watershed function. Each patch, at any level, is at once an integral whole and a part

of a higher-level component (Koestler 1967).

Landscapes have a special kind of vertical structure: they are nested spatially. Each level of the hierarchy contains the levels below it. This property of containment provides for a number of special features (Allen and Hoekstra 1984). Levels in a nested hierarchy may coincide when defined by a variety of ordering criteria or measured attributes. Forest gaps might be recognizable in terms of species composition, biomass, ambient sunlight (insolation), or other attributes. They might also be recognizable in terms of the limited basic resources that constrain tree growth. Thus, the hierarchy is also ordered on the criterion of constraint.

Indeed, it seems that constraint and interaction can be mutually reinforcing as ordering criteria: patches delineated by a spatially distributed constraint (e.g., topographic moisture) may interact to generate higher-level aggregates. Forest stands defined on topographic moisture may be joined by seed dispersal to generate an interacting landscape mosaic. As a further consequence, note that because landscapes contain stands, higher levels of this hierarchy are larger than lower levels; also, because stands interact more within themselves than among themselves, higher levels are slower than lower levels. This special relationship among ordering criteria in a landscape hierarchy makes its structure very robust. The hierarchical levels are often evident as patches in nature.

Each hierarchy is constructed in

relation to a specified phenomenon of interest. Different phenomena may call for differences in the hierarchies we use to study them. While the hierarchy, gap-stand-watershed-landscape, might be appropriate for a study of either species composition or nutrient cycling in forests, these levels need not be relevant for other purposes. For a landscape dominated by recurrent fires, hierarchical levels corresponding to the scales of individual fires and to the larger fire-mosaic might be a more appropriate conceptualization. For a study of forest birds, an obvious focal scale would be territories. The higher levels, for example, the forest stand, may or may not be suitable to studies of fires and birds. Thus, the species-composition hierarchy for a forest system is not the only one possible.

Mechanistic explanation. The behavior of a forest gap through time depends on the individual trees in the gap. Their growth rates, lifespans, shade tolerance, response to moisture and nutrient levels, and initial sizes collectively determine which trees come into dominance and which trees are suppressed. Gaps, in turn, interact to generate stand dynamics. Whether sugar maple (*Acer saccharum*) will become more important than white oak (*Quercus alba*) in a particular stand may depend on the interaction of nearby gaps. If oak-dominated gaps tend to become maple-dominated gaps as a result of seed rain from nearby maples, stand composition will shift toward maple. This general rule carries upscale: stands, then watersheds, then landscapes interact to generate successively higher-level behaviors.

We can go a long way toward understanding a complex phenomenon when we explain its behavior in terms of interactions among its parts. But understanding a hierarchical phenomenon requires more than mechanisms. Understanding requires that the mechanisms be considered in context.

Constraint and higher-level context. Specific conditions within the gap influence the processes, such as tree growth and longevity, that generate gap dynamics. The pattern of available light in the gap, for example,

provides a context that constrains individual tree growth, usually limiting replacement of a dominant tree to shade-tolerant species. This knowledge may not, however, allow us to predict with certainty which shade-tolerant species will come into dominance: it might be sugar maple, or beech (*Fagus grandifolia*), or basswood (*Tilia americana*), or some other equally tolerant species. The greater the functional redundancy among trees, the less predictable is case-specific behavior. The constraint in effect judges all trees by a single standard.

Some other constraints on tree growth are soil moisture levels, nutrient availability, and disturbance regimes such as fires or wind. All these constraints affect the trees within the gap, favoring some over others. The constraints sort individually since trees differ individually with respect to such characteristics as fire tolerance, drought tolerance, and ability to withstand wind.

The factors producing these constraints are themselves patterned on some spatial scale. Topographic pattern governs soil factors, insolation, and moisture and defines the characteristic spatial scale of these constraints. Each of these constraints provides a context for the behaviors of the lower levels of the hierarchy.

Nested hierarchical organization further specifies the context for lower-level behaviors. Returning to the example of tree species replacement in gap dynamics, we might not be able to specify precisely which tree will come into dominance, but we can predict that it will be a species that is well-represented in the local seed pool and that has not been excluded by the other constraints acting on that particular site. Collectively, the various constraints provide a context that allows us to make sense of what we observe in the forest at a given time, a contextual explanation. In general, the more constraints we consider at one level that are relevant to one criterion, the greater our predictive power.

Thus, to understand a complex, hierarchically organized system we must consider multiple levels. The reference level is the scale on which the phenomenon is witnessed as an interesting event. Once specified, the event has its mechanistic explanation

at the next lower level, and its significance in the context of higher-level constraints (O'Neill et al. 1986).

Hierarchy as an analytic tool. Simultaneously considering a complex ecological system on many scales is an intimidating prospect that is made simpler by the manner in which patterns translate across hierarchical levels. Hierarchy isolates the phenomenon of interest. In a forest, a tree integrates fine-scale variation in its physical environment, experiencing only a blend. For example, a tree's growth ring is an integration of growing conditions during the year, and it is an instant cross-section of any longer-term trends. In addition, a tree experiences large patterns as a relatively constant context. Each tree within a gap is not subject to the full range of soil patterns in a watershed, but only to the small sample of such patterns that constitute the local condition.

A component at a given level of a hierarchy experiences as variable only those patterns that are similarly scaled in rate, as well as in size. By comparison lower-level dynamics are so fast that they are experienced as average values; higher-level dynamics are too slow to be experienced as variable. Thus, the complexity of dynamics and spatial patterns at several scales is resolved into a few variables and a set of constants, defined relative to the reference level.

A powerful consequence of a hierarchical paradigm is that it allows one to focus on an event at a particular scale, while recognizing that there are other scales relevant to that event. When describing an event, its characteristic scale dictates an appropriate sampling scale and frequency. The scale of an event defines the observational level through which the rest of the hierarchy is accessed. The next lower level provides the components of the event and its mechanistic explanation. Higher levels provide the context that gives the event greater significance. These higher-level factors can be treated as constants when viewed from the reference level, though they may be quite variable at larger scales.

Levels of the hierarchy further removed from the reference level are not of immediate concern, in that they contribute very little toward un-

derstanding the event of interest. For example, in describing gap dynamics, we know that safe sites for germination are important to seedling establishment. However, we need not consider these details at the level of the gap, because within gaps safe sites occur with predictable frequency. We also know that the specific forest exists because the post-Pleistocene climate favors trees, but this knowledge has little bearing on the event at hand.

To recap, a hierarchical perspective would emphasize three strategic concerns in an analysis of landscape pattern: (1) to detect pattern and define its spatial and temporal scale, which is to define functional patches at a specific level; (2) to infer which factors generate the pattern, whether they be demographic processes, environmental constraints, disturbances, or a combination of these; and (3) to relate this pattern to adjacent levels. We have emphasized that the notions of mechanistic interaction and constraining context explicitly involve multiple levels of reference. In the next section we pursue a variation on this theme.

Consequences of landscape pattern

We have seen that the apparent complexity of landscapes can be partially resolved by decomposing them into a hierarchical framework. It is when one considers landscape phenomena at different levels that the consequences of pattern at characteristic scales emerge. These consequences are far reaching; reviews by Levin (1976a) and Wiens (1976) illustrate the scope of the subject. One fundamental consequence of hierarchical structure is that events causing pattern on one scale can be incorporated into higher-level behavior (O'Neill et al. 1986). Through this incorporation, effectively nonequilibrium dynamics or spatial heterogeneity at one scale can be translated to equilibrium or constancy at a higher level.

There are two aspects of incorporation that are especially pertinent to landscape ecology. The first concern is whether the biological mechanisms necessary to a pattern disturbance at a given scale are available in the system; that is, do the mechanisms exist? Obviously a logical consequence of

patchiness would be the evolution of mechanisms to deal with it. Both plants and animals have evolved diverse tactics to utilize patchily distributed resources. One strategy for dealing with patchiness is to employ superior competitive ability to persist within a given patch, maybe even exerting some control over the environment. An alternative strategy is to concede competitive advantage by playing the role of fugitive on a larger scale.

The cherry (*Prunus* spp.), which requires open sites for regeneration, is a fugitive in both time and space (Auclair and Cottam 1971, Marks 1974). Cherry seeds may be dispersed great distances by birds, and at the site of deposition, the seeds may remain viable for several decades. Thus, cherry can take advantage of an appropriate regeneration site elsewhere, or it can await the recurrence of a disturbance that brings an appropriate site to it. At the level of gap dynamics, cherry is a loser: it is eventually replaced by longer-lived, shade-tolerant species. But the cherry maintains a nearly constant abundance

over the landscape, although not at specific local sites. Cherry wins the war, though it loses every battle. Thus the dynamics of regional patchiness are incorporated at a higher level.

That species assemblages in nature can be categorized into types (constant assemblages) at a variety of scales (e.g., Braun 1950, Holdridge 1967, von Humboldt 1807) suggests that many natural patterns are incorporated by ecological systems. In particular, a disturbance regime that can be incorporated is not disturbing at all (Allen and Starr 1982). At a higher level, disturbance frequency can be viewed as a constraint that governs an equilibrium species assemblage. An analysis of prairie plant species composition in response to fire illustrates this two-level approach. Allen and Wyleto (1983) used the "time since fire" variable to emphasize the successional dynamics of plant species composition following a burn. Using the "fire frequency" as a variable, they demonstrated that different equilibrium species assemblages were maintained under different fire regimes. In effect, data transformation

changed the level of resolution in the data, and accessed a hierarchical system at two different levels (Allen et al. 1984).

Incorporation can be passive; a disturbance is incorporated simply by increasing the scale of reference. In the example of cherry abundance, the cherry does not affect the regional disturbance regime. In other cases, adaptive mechanisms may evolve such that the disturbance regime is actually modified. Many fire-adapted systems evolve such that the member species produce volatile substances and serotinous seeds, which require the heat of a fire to germinate. These species both exert some control over fire frequency and capitalize on fires for episodic regeneration (Mutch 1970). This incorporation with evolutionary integration has repercussions that we will discuss later.

A second aspect of incorporation pertinent to landscape ecology concerns whether incorporation can be realized within a particular bounded system. That is, given a geographically defined region (e.g., a park) and the perturbation affecting it, is the region of sufficient scale to incorporate the disturbance? Shugart and West (1981) have addressed this idea, using a forest simulation model. In their simulations, individual trees suffered stochastic, age-related mortality, and each model plot (0.08-ha gap) was independent of other plots. They found that 50 model plots were necessary to stabilize the statistical variance in biomass associated with gap dynamics, that is, to incorporate gap dynamics using biomass as a standard.

Shugart and West then compared several bounded landscapes to the scale of their disturbance regimes. They defined a quasi-equilibrating landscape as one in which the area ratio of bounded landscape to disturbance regime was at least 50:1. Smaller landscapes were called effectively nonequilibrating (Figure 4).

A bounded landscape that is large enough to incorporate the factors that disturb its component patches has a constant frequency distribution of patches of all types at all times, and is considered to be a strictly equilibrating landscape. A smaller landscape that is unable to incorporate a disturbance has a transient frequency distribution of patch types, which changes

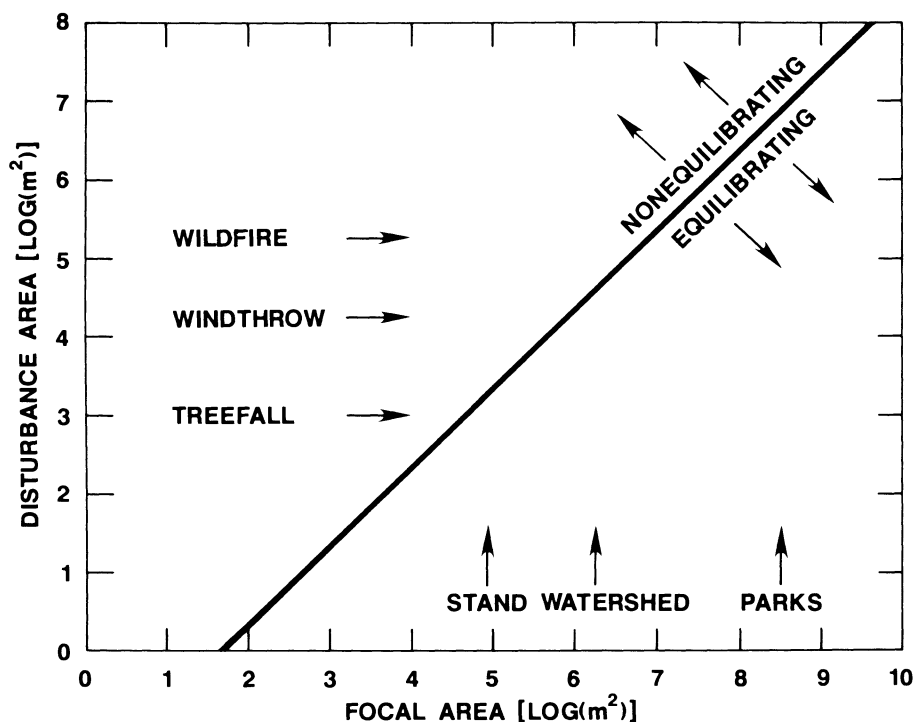


Figure 4. Classification of landscapes relative to the spatial scale of their disturbance regimes, according to a 50:1 ratio as calculated for forest biomass dynamics (Shugart and West 1981). A forest stand may incorporate single treefalls but not larger windthrows or fires; a small watershed can incorporate treefalls but perhaps not larger windthrows, and not wildfire; a larger park may incorporate all of these disturbances.

ANTHROPOGENIC EFFECTS ON LANDSCAPES

in response to each disturbance event. These are called nonequilibrating.

The implication is that the relative abundance of each patch type can be predicted readily at the higher level, if the lower-level dynamics can be incorporated. In a national park that is large enough to incorporate wildfire, a constant and predictable proportion of fire-successional vegetation (perhaps critical habitat for some species) is maintained. Conversely, a park that is too small to incorporate a natural wildfire regime does not lend itself to straightforward predictions of the relative abundance of patch types.

The phenomenon of incorporation is a natural extension of pattern at characteristic scales (O'Neill et al. 1986). This perspective is especially illuminating when applied to man-dominated landscapes.

Man-dominated landscapes

There is a tendency to view man-dominated landscapes as being different from natural landscapes. Excellent discussions of human impacts on landscapes are available (Burgess and Sharpe 1981, Forman 1981, Forman and Godron 1981 and 1986, Mooney and Godron 1983). We focus here on man's influence on the characteristic scales of landscape phenomena.

Effects of anthropogenic scaling. A primary influence of man is to rescale patterns in time and space (Figure 5). Human control of forest fires illustrates several ramifications of this rescaling. Fire suppression retards the natural frequency of burns in systems that have incorporated fire. When wildfires do occur as a result of fuel buildup, they may escape to burn over a larger area and at a greater intensity than they would otherwise. A thick-barked tree that could survive a low-intensity fire might succumb to a hotter fire. A species with seeds that require episodic fires in order to regenerate might decrease in regional abundance because fire suppression removes opportunities for germination. In each case, an incorporating mechanism has been short-circuited.

Under the constraint of periodic burns, the role of a fugitive, like the cherry, might have a winning strategy at the landscape scale. With fire suppression, the constraining rules

HUMAN ACTIVITY	CONSEQUENCES
RESCALE PATCH DYNAMICS	RENDER ADAPTIVE MECHANISMS LESS EFFECTIVE CHANGE CONSTRAINING RULES ALTER PATCH INTERACTIONS
RESCALE BOUNDED REGIONS	REDEFINE FROM EQUILIBRATING TO NONEQUILIBRATING STATE
INTRODUCE NOVEL PATCHES AND DYNAMICS	RENDER ADAPTIVE MECHANISMS LESS EFFECTIVE REDUCE POTENTIAL FOR SPECIES TO EVOLVE ADAPTIVE MECHANISMS
HOMOGENIZE PATTERNS THROUGH LAND USE	REDUCE TREE SPECIES DIVERSITY REDUCE HABITAT DIVERSITY FOR FOREST WILDLIFE

Figure 5. Summary of the effects of anthropogenic rescaling of natural landscape patterns and processes.

change and that role may no longer be advantageous. Finally, small burns in a fire mosaic might depend on an immediate seed rain from adjacent unburned forest in order to regenerate. Rescaling the burns to cover larger areas might decrease the influx of seeds, slowing the regenerative dynamics of the mosaic. Though these effects are not independent, the specific actions of rescaling are (1) to render natural incorporating mechanisms less effective; (2) to change the set of constraints (including disturbance frequencies) governing lower-level biotic processes; and (3) to change the degree of interaction among patches, thus altering behaviors that influence higher levels.

Man also rescales natural regions by establishing new boundaries. Pipelines, drainage canals, and roads all set new bounds if they are effective barriers to patch interactions, especially species dispersal. This is critical when the scale is redefined relative to the scale at which disturbances can be incorporated. In such cases, an equilibrating system may be rescaled to a nonequilibrating state. Forest fragments in the eastern United States illustrate this effect. Some fragments are large enough to incorporate disturbances; most are not (Pickett and Thompson 1978).

Man also introduces novel pertur-

bations that might differ in spatial or temporal scale from natural regimes. For example, the spatial scale and dynamics of human land use may be different from any natural forest process. Many changes in land use cover large areas but are frequent or chronic, contrary to the natural rule of large/slow or small/fast. Man-dominated landscapes may change according to such nonecological factors as price of commodities or transfers of land ownership. One would expect that such anthropogenic regimes would disrupt the natural system, leaving only behaviorally plastic species. This is consistent with the frequent association of generalists and weeds with man-dominated regions.

Man's activities at some scales may homogenize a forest stand's fine-scale patterns that result from gap dynamics. Chronic use of woodlots for grazing or as a fuelwood source can obliterate natural patterns in regeneration, so that the entire woodlot assumes a high degree of similarity. Such an effect can be indirectly imposed by natural edge effects in very small woodlots. In small woodlots, increased insolation and convection can alter the physical environment to such an extent that natural gap-phase replacement mediated by shade and moisture is not expressed. Very small woodlots do not develop an interior

of mesic species; they remain essentially all edge (Levenson 1981). This has an obvious effect on local and regional forest diversity (Noss 1983) but may have further consequences. The regional abundance of many forest birds and small mammals may depend on a continual availability of specific forest microhabitats (Seagle et al. 1984, Whitcomb et al. 1981). Man's homogenizing effect may thus contribute to a regional decline in forest microhabitat specialists.

Man's various effects on landscape pattern are neither exclusive nor independent but are typically interactive and cumulative. A forest fragment has an imposed size. It may have its component events rescaled and its internal patterns altered. It may be operating under a new or rescaled set of higher-level constraints. Each of these factors contributes to the confounded and confounding behavior of woodlots (Burgess and Sharpe 1981, Curtis 1956, 1959).

Prescriptive scaling in land management. A knowledge of the characteristic spatial scale and natural frequency of patch dynamics on a landscape lends itself to prescriptive applications in natural resource management. In general, resource management should be scaled to mimic natural patch dynamics, so as to take advantage of preselected adaptive mechanisms in the local species pool. Foresters use prescriptive scaling when they mimic natural disturbances with clearcuts, a practice that represents the collective wisdom of generations of foresters, who have found a successful clearcutting strategy through trial and error. A hierarchical approach dictates the same strategy deductively. It seems likely that the mimicry approach to resource management should prove useful in other land use applications.

Another method of prescriptive scaling might capitalize on the notion that lower-level interactions are propagated upward in a hierarchy to generate higher-level behaviors. This suggests that management could be tailored such that a minimal amount of management, at the proper time and place, could be amplified at higher levels to have maximal effect. One might envision steering long-term, large-scale forest dynamics by

thoughtfully cutting or planting just a few trees.

A third mode of prescriptive scaling proceeds from our discussion of incorporation. We suggest that an inherently nonequilibrium landscape that cannot incorporate its internal dynamics can be equilibrated by rescaling its internal dynamics to effect smaller patches. Thus, prescribed burning of small patches could reinstate fire into a park that could otherwise not incorporate wildfire. In rangelands, controlled rotation of grazing pressure in small paddocks mimicks but rescales the natural regime of far-ranging herbivores, effectively creating rangeland microcosms. It seems fruitful to attempt to generalize these familiar examples to other systems in managed landscapes.

Experimental landscapes. Man-dominated landscapes can provide natural experiments from which we can learn a great deal about ecological scaling in natural systems. Human land-use patterns may be more variable than many natural environmental patterns, because human land use reflects not only natural constraints (Bowen and Burgess 1981) but also the financial resources and personal whims of private landowners. Thus, these landscapes often provide a spectrum of anthropogenic patches of various sizes within the same area (e.g., Ambuel and Temple 1983, Burgess and Sharpe 1981, Forman et al. 1976). Such landscapes can provide the necessary empirical observations from which to infer critical thresholds of interaction among components of hierarchical phenomena. Specifically, studies of man-modified landscapes may indicate how inter-patch distance, connectivity, and spatial configuration modify patch interactions to generate higher-level behaviors in mosaics; what the minimum difference in scale might be for a perturbation to be incorporated at the next higher level; and whether these rules are constant or vary systematically for different kinds of phenomena. We suggest that general answers to such questions will form the basis of a theory of landscape ecology.

Conclusion

The purpose of a paradigm is to serve

as a conceptual and analytic model to be exercised as long as it is useful. That hierarchy theory is conceptually appropriate to landscape ecology should be apparent from our discussion. We have stated very little that is actually novel: we have merely rephrased familiar notions in terms of patterns at characteristic scales. Indeed, several early classics (e.g., Tansley 1935, Watt 1947, Whittaker 1953) and a host of more recent efforts (Allen and Starr 1982) embrace ideas that are implicitly hierarchical. Hierarchy theory takes this conceptually good fit and pushes it deductively toward new insights into complex, natural phenomena. As a nascent interdisciplinary endeavor, landscape ecology can benefit from a hierarchy theory as a unifying conceptual and analytic framework.

Acknowledgments

This research was sponsored by the National Science Foundation's Ecosystem Study Program, under Interagency Agreement No. BSR-8103181-A02 with the US Department of Energy, under Contract No. DE-AC05-84OR21400 with Martin Marietta Energy Systems, Inc. Publication No. 2807, Environmental Sciences Division, ORNL. We appreciate the helpful comments of T. F. H. Allen, B. Milne, D. Miller, P. Delcourt, D. DeAngelis, and A. King.

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