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Landscapes, space and equilibrium: shifting viewpoints

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Abstract: The classical view of ecological systems has been one that assumes a state of equilibrium and stability; this is encapsulated in the 'balance of nature' paradigm. Over the last 30 years ecologists and biogeographers have rejected the view that ecological systems are inherently stable or at some sort of equilibrium. Instead a nonequilibrium view, emphasizing the role of chance events such as disturbance in ecological dynamics, has become dominant. Alongside this change, the way in which the roles of space and spatial heterogeneity in ecological dynamics are viewed has shifted. Classical ecological theory tended to ignore spatial dynamics and heterogeneity and focused instead on temporal pattern. Over the last 20 years this view has also changed and the importance of spatial pattern has been emphasized. Through the explicit consideration of space and spatial pattern it has been shown that spatial heterogeneity may act to either stabilize or destabilize ecological systems and processes. This paper reviews these two changes in the way ecological systems are conceptualized and explores how they are inter-related. Advances in our understanding of the role of space and the nature of equilibrium in ecological systems are discussed within the context of both modelling and empirical studies, as are the problems involved with experimentally testing the large body of spatial theory developed.

Key words: disturbance; equilibrium; landscape ecology; scale; spatial models; spatial pattern; succession.

I Introduction

Over the last three decades, ecologists and biogeographers have profoundly altered their views on how ecological systems are best conceptualized. Until the early 1970s ecology was dominated by a 'balance of nature' view in which systems were expected to be at equilibrium (Botkin, 1989). This concept has a very long history, and although in modern ecology it can be dated back to Clementsian ideas of succession, it is evident in the writings of philosophers such as Aristotle (384–322 BC) and in the thinkers of the Renaissance and the Age of Enlightenment. Most ecologists and biogeographers have now, to a lesser or greater degree, rejected this framework in favour of a

nonequilibrium approach in which chance events such as disturbance play crucial roles in structuring ecosystems at multiple scales. Alongside a switch from an equilibrium to a nonequilibrium view there has been a change in the way that space is considered in ecological theory. Despite some seminal early works (e.g., Watt, 1947; Huffaker, 1958), spatial heterogeneity was largely ignored by theoretical ecologists on the grounds that it compromised the assumptions of equilibrium that were made; it also led to technical difficulties in the formulation and solution of the analytical models being used. Instead, the emphasis was very much on the *temporal* dynamics of ecological systems. A growing recognition in the 1970s (e.g., Levin, 1976) that spatial heterogeneity influences ecological processes at multiple scales came at much the same time that the shift away from the equilibrium framework was occurring, and the two are related. Although ideas of equilibrium and stability were amenable to theoretical and empirical analysis at that time, approaches to spatial analysis lagged behind for several reasons (such as the logistical and technical challenges of conducting 'spatially explicit' ecological research). This review outlines the key changes in issues of equilibrium in ecosystems and the emergence of 'spatial ecology', and attempts to link the two. Although the issues considered are not solely limited to ecology (for example the consideration of space in hydrological models has paralleled developments in ecological models – see Moore *et al.*, 1991) they are considered here in that light and especially within the context of landscape and disturbance ecologies.

II The conceptualization of space in biogeography and ecology

Traditionally ecology has adopted a largely homogeneous view of space. Attention has been focused upon and within small areas (e.g., metre square quadrats, watersheds etc.) and it has been assumed that ecological interactions are spatially uniform. The reasons behind the adoption of this view are many, but are largely centred on a desire to keep theoretical and experimental studies relatively simple (Wiens, 1997). The classical approach to modelling ecological systems ignores space by assuming that every individual is equally accessible to every other individual. The resulting model takes the form of a series of difference or differential equations for the mean abundance of the various types. Because every individual is assumed to see the average or mean-field, this approach is termed the 'mean-field' solution (Hastings, 1994). Although it was realized that spatial heterogeneity is ubiquitous (e.g., Watt, 1947) it was assumed to be irrelevant in determining the patterns of interest (Levin, 1992). Indeed, if ecosystems are perceived as homogeneous and their dynamics can be explained using equilibrium models then the explicit addition of spatial heterogeneity becomes problematic (Kareiva, 1990). Over the last 15–20 years, as spatial heterogeneity has been explicitly incorporated into many ecological field studies and models, it has become obvious that it is important in many situations. For example, species diversity within an area may be related to habitat heterogeneity (Tilman, 1994), the dynamics of populations and predator–prey interactions may be more stable or persistent in patchy environments (Kareiva, 1990; Hassell *et al.*, 1994), the spread of contagious disturbances such as fire or pathogen outbreaks is altered by patchiness (Turner and Romme, 1994; Li and Apps, 1996; Logan *et al.*, 1998) and dispersal and recruitment dynamics are affected by the patch structure of the environment (Pulliam, 1988; Pulliam and Danielson, 1991; Wiens

et al., 1993; Bond *et al.*, 2000). Furthermore, the inclusion of a spatial dimension into ecological models has also shown that spatial heterogeneity can evolve in otherwise spatially homogeneous systems. It has been demonstrated that the spatial nature of processes such as dispersal even in an otherwise homogeneous landscape is sufficient to cause pattern to arise (Tilman *et al.*, 1997; Huxel and Hastings, 1999).

Much of the focus on spatial heterogeneity has been on the development of a patch mosaic theory, in which ecological dynamics within and between patches embedded in a featureless background (the landscape 'matrix') are compared with those generated from models assuming spatial heterogeneity. Spatially extended optimal patch foraging theory (Ritchie, 1998), source-sink models (e.g., Pulliam, 1988; Pulliam and Danielson, 1991; Doak, 1996) and metapopulation dynamics (e.g., Hanski, 1991; Hanski and Simberloff, 1997) are all based on these ideas. Recently, however, it has been recognized that the matrix plays a more important role in between-patch interactions than had been previously acknowledged (Ricketts, 2001). A second focus of attention has been heterogeneity and the effects of spatial variance, rather than patch interactions, on ecological patterns and processes (Hurlbert, 1990; Horne and Schneider, 1995). A third area of activity has been patch dynamics, in which systems are viewed as mosaics of patches generated by disturbance (see Parker and Pickett, 1998). Patch dynamic theory has focused on the way in which the spatial patterns and relationships of patches in a matrix change through time (see Pickett, 1978; Pickett and White, 1985a; Wu and Loucks, 1995). Shifting-mosaic or wave-regeneration vegetation succession provide examples of this approach (e.g., Wissel, 1991).

Landscape ecology has attempted to synthesize the various approaches to spatial heterogeneity through an emphasis on the explicit spatial structure of entire, heterogeneous mosaics, the interactions among the patches in the mosaic and the dynamics of mosaic structure over time (Turner *et al.*, 1989a; Wiens *et al.*, 1993). Hierarchy theory suggests that landscapes are organized into patterns within a hierarchy of spatial and temporal scales (O'Neill *et al.*, 1986), and this conceptualization of landscape structure has been an important part of the development of landscape ecology (Urban *et al.*, 1987). Hierarchy theory predicts that the organization of pattern within a hierarchy of spatial and temporal scales is a reflection of a hierarchy of process rates (Cullinan *et al.*, 1997). Numerous ecological and anthropogenic disturbances maintain landscape patterns or set into motion the creation of new landscape patterns across a range of spatial and temporal scales (Pickett *et al.*, 1989; Kareiva and Wennergren, 1995). As a result the landscape may be viewed as a collection of patches undergoing successional change, each at different points in successional time, reflecting their varied disturbance histories; the so-called 'landscape mosaic' (Christensen, 1993).

It is obvious that an understanding of patchiness and spatial heterogeneity in the landscape also requires a conceptual framework for the understanding of boundaries. Boundaries are the entities that define patches, and it is patchiness that causes spatial heterogeneity (or conversely, spatial heterogeneity is expressed as patchiness) (Wiens *et al.*, 1985; Wiens, 1992). Boundaries may be very variable in form, ranging from sharp divisions (such as the edge of a fire scar) to fuzzy continuums, and shape, ranging from linear to diffuse or convolute. These differences affect flows across the boundary and may be influential in determining landscape dynamics and processes such as the spread of contagious disturbances (Turner, 1989; Wiens, 1989). DeAngelis and Waterhouse (1987) argue that heterogeneity resulting from patches and boundaries increases a

system's variance, thereby reducing its predictability. It may not be possible to understand the dynamics of a system comprised of many patches simply through averaging across all patches; instead the patch-boundary configuration may lead to spatially dependent trajectories as a result of the spatial nature of interactions within the system (DeAngelis and Waterhouse, 1987; Wiens, 1992).

The scale (grain and extent) at which patches and boundaries are viewed alters the perception of the nature of spatial heterogeneity in any system; for example, complex, fine-grained mosaics may disappear as the scale at which they are viewed is altered in either direction (Turner *et al.*, 1989b). Hence, the grain at which the system is viewed will alter the ability to detect boundaries, depending upon the scale of the discontinuity that defines them. Nevertheless, ecotones and boundaries detected at typical 'human' scales are not the only such features existing in a system, and whether these are the appropriate scales at which to view systems is dependent both upon the processes and organisms of interest (Addicott *et al.*, 1987; Wiens, 1989). For example, Lord and Norton (1990) argue that fragmentation occurs across a full continuum of scales in many different domains, and that although conservation biology has largely focused on coarse-grained, or geographic, fragmentation (kilometres), fine-grained, or structural, fragmentation (metres) may be equally as significant for many processes and organisms.

Central to spatial and landscape ecology is the idea that there are strong feedbacks, in both directions, between (spatial) pattern and (ecological) process. For example, in a landscape disturbed by fire not only does the spread of fire generate pattern at the landscape (and other) levels due to the effects of topography and so forth, but this pattern influences the spread of subsequent fires (Turner and Romme, 1994). As will be discussed later, in some ways this patch structure causes the landscape to have a 'memory' (Hendry and McGlade, 1995; Holling *et al.*, 1996). The interactions between pattern and process have been considered in some detail in several model-based studies. In a simple cellular automata model of interspecific competition for space between five grass species, Silvertown *et al.* (1992) found that markedly different competitive outcomes occurred depending only upon the initial arrangement of species in the model (see Figure 1). Simple manipulation of pattern could lead to complex, nonlinear dynamics, with transitory increases followed by decreases in species' abundance. Community change followed trajectories that could not be deduced in any simple manner from knowledge of pair-wise interactions alone. The importance of these findings is the suggestion that the spatial pattern and configuration of competing species may be just as important as the density and frequency of competitors in determining the outcome. The model of Silvertown *et al.* (1992) was further analysed by Durrett and Levin (1998) who found considerable differences between nonspatial and spatial forms of the model. In a similar context, Chesson (2000a, b) shows how nonlinearities in competitive ability that may be crucial in coexistence are only evident when space is explicitly considered.

III Concepts of equilibrium and stability in ecological systems

As described in the preceding section, ecology, largely for reasons of analytical convenience, has tended to view ecosystems as being at equilibrium, largely ignoring

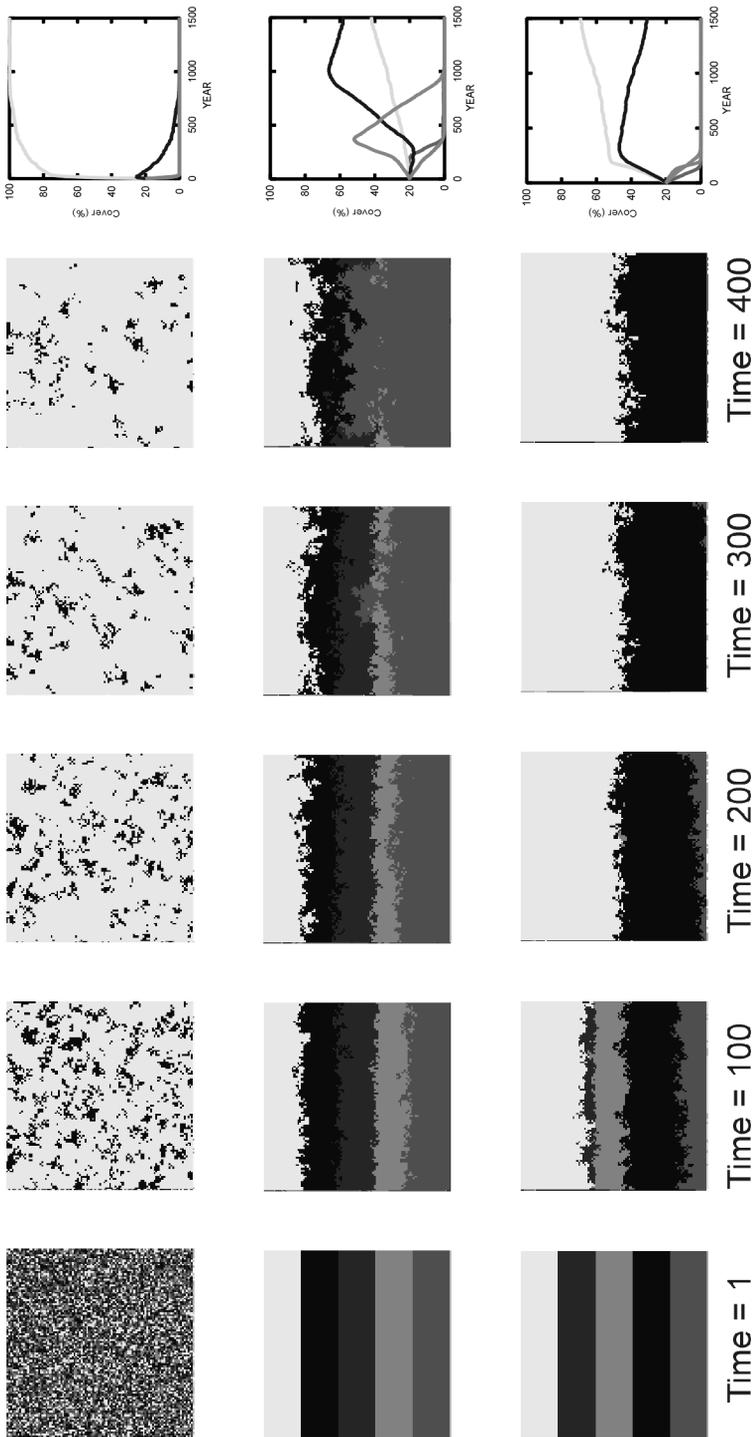


Figure 1 The effects of initial spatial arrangement on competitive outcomes and community dynamics in a five-species competition model based on that of Silvertown *et al.* (1992). It can be clearly seen that the initial configuration of the five 'species' has dramatic effects on the community dynamics that may persist over long time periods

space and spatial heterogeneity. Alongside the changes in conceptualization regarding the importance of space, has come a gradual change in the way in which disturbance, succession, stability and equilibrium in ecosystems are viewed. This section outlines the development of the conceptualization of how disturbance and succession operate in the landscape and, in particular, the issue of whether landscapes are ever at equilibrium (and the scales at which equilibrium might be a useful concept). Finally, the idea of spatial self-organization in the landscape is discussed.

1 'Classical' views of equilibrium and stability

Myriad definitions of 'stability' have been advanced in an ecological context. In a recent review of the concept, Grimm and Wissel (1997) found 163 definitions of 70 different stability concepts. They comment (p. 323) that the term 'stability' is so vague as to be meaningless and suggest its replacement by three alternative stability properties: (i) constancy (staying essentially unchanged), (ii) resilience (returning to the reference state (or dynamic) after a temporary disturbance) and (iii) persistence (persistence through time of an ecological system). Although 'constancy' and 'persistence' may initially appear the same they differ in that the former refers to some reference state or dynamic (e.g., equilibrial, oscillatory, etc.), whereas the later refers solely to the persistence of the system irrespective of state or dynamic. Part of the problem with defining the concepts of equilibrium and stability has arisen from an inappropriate application of stability concepts derived from mathematics and physics; such concepts usually characterize simple dynamic systems. As will be discussed below, issues of spatio-temporal scaling are also central to ideas of stability and equilibrium.

The classical ('balance of nature') view of stability has been one of dynamic equilibrium (the so-called steady state) that admits systems can deviate from equilibrium, and that the equilibrium may be unstable with the system cycling around it (DeAngelis and Waterhouse, 1987). Nevertheless this perspective has at its centre the idea that every system has some equilibrium state. Pickett *et al.* (1994) identify five characteristics of equilibrium systems: (i) they are basically closed, (ii) they are self-regulating, (iii) they possess stable point *or* stable cycle equilibria, (iv) they have deterministic dynamics, and (v) they are essentially free of disturbance and other stochastic structuring events. Conversely, from a nonequilibrium perspective, ecological systems are considered to be open and controlled by both extrinsic and intrinsic factors. Furthermore, nonequilibrium systems lack a stable equilibrium point and are not deterministic, with stochastic events such as disturbance being regarded as integral components of the system. If equilibrium is observed it may only be seen at certain spatio-temporal scales (Pickett *et al.*, 1994).

The prevailing view in ecology in the first half of the twentieth century was that ecosystems progressed steadily along some well-defined successional pathway to a stable, self-sustaining climax state, and that both the pathway and the climax state were entirely predictable (McCook, 1994). In terms of the definitions provided above (Pickett *et al.*, 1994; Grimm and Wissel, 1997) the climax state conforms to all the properties of a stable or equilibrium system. The composition and structure of early successional communities was assumed to be a function of local site conditions, the result of which would be a diverse group of early successional seres. Alteration of the environment by

plants in seral communities diminished variability in the landscape, with the result that the biotic and abiotic environment converged on a climax state determined largely by regional climate (Sprugel, 1991). Several points are implicit and explicit in this classical theory of vegetation change (Christensen, 1993): (i) successional change is largely autogenic (i.e., change is the result of groups of organisms changing the environment such that it becomes favourable for invasion by other groups of organisms), (ii) assemblages of organisms comprising climax communities have coevolved over long periods, (iii) in the absence of disturbance, variations among the communities on the landscape should diminish over time, and (iv) successional change is a linear and directional process leading to a stable endpoint. Because of its emphasis on autogenic processes, disturbance events were considered to be allogenic. Indeed Clements (1916, 1928, 1936) and other early successional theorists considered disturbance to be unnatural and usually the result of recent human modifications of the landscape. Furthermore, since stability was assumed to increase over successional time, the likelihood of disturbance events occurring was assumed to diminish.

Over the second part of the twentieth century it became obvious, however, that disturbance events are an integral component of most (if not all) ecological systems, and that natural disturbances are so common that they prevent ecological systems from reaching a stable climax (White, 1979; Sousa, 1984). Although adequately defining 'disturbance' has proved problematic (Rykiel, 1985), White and Pickett's (1985) definition of disturbance as '...any relatively discrete event in time that removes organisms and that changes resources, availability of space or the physical environment' has been widely adopted. If disturbance is ubiquitous it becomes unrealistic to assume that climax is the 'normal' condition for an ecological system. Although it had become clear that disturbance was an essential and inevitable process in most ecosystems, the idea that they are highly regulated cybernetic systems was still compelling (O'Neill *et al.*, 1986), and much debated (e.g., cf. Engelberg and Boyarsky, 1979; Patten and Odum, 1981).

2 Recent concepts of landscape equilibrium and change

Based on observations of gap dynamics in a number of different systems, Watt (1947) described how small (i.e., tree-sized) areas undergo repeated and predictable temporal patterns following disturbance events such as treefalls. Expanding on this, Watt realized that in a landscape comprising many smaller elements, each in a different stage of the gap dynamics cycle, each stage of succession would be represented somewhere in a sufficiently large area at any given time. Watt (1947) proposed the idea of the 'unit pattern' – the full representation of this temporal pattern in all its phases. He noted that the abundance of each phase in the landscape should represent its duration and that (p. 19) 'departures from this phasic equilibrium either in space or in time could then be measured and correlated with the changed factors of the environment'. The unit pattern concept represents one of the first attempts in ecology to link spatial and temporal pattern explicitly. The idea of the unit pattern was expanded upon by Whittaker (1953) as the 'climax pattern', and in the 'shifting mosaic steady-state' concept proposed by Bormann and Likens (1979a, b). Whittaker's climax pattern attempts to incorporate both Clementsian and Gleasonian views of succession and, in essence, overlays the unit

pattern on a heterogeneous physical landscape. The 'shifting mosaic steady-state' conceptualizes the landscape as a system in which, although the vegetation present at specific points in the landscape is dynamic, the proportion of the landscape in each successional stage remains invariant (see Figure 2); in other words, the landscape is stationary.

The models outlined above all represent equilibrium views of the landscape (albeit somewhat scale-dependent) and have proved difficult to test empirically. In the case of fire, the idea that the likelihood of disturbance may increase during succession led to the ideas of pulse stability and the fire cycle (see Loucks, 1970); the fire cycle concept views the landscape as stationary with episodic perturbation. Loucks suggested that communities might appear unstable at any point in time as a result of change(s) in community composition but that the entire long-term sequence of changes constitutes a stable system because the same changes occur after every event. In fire-dominated systems, for example, the statistical distribution of the patch age structure of the landscape mosaic and the time intervals between successive fires may be calculated (van Wagner, 1978; Johnson and van Wagner, 1985; Johnson and Gutsell, 1994). This approach explicitly recognizes the stochastic nature of disturbance regimes, but assumes that the distribution of the return interval and the proportional composition of the landscape remain approximately constant over time. However, Clark (1989, 1991a, b) demonstrates that the temporal distribution of disturbance intervals may not be constant, and the likelihood of disturbance may vary with the time since the last disturbance event.

With its emphasis on the feedback between disturbance regime and landscape structure the fire cycle concept provides a useful way of conceptualizing the role of disturbance in the landscape. However, it is an oversimplification to view these

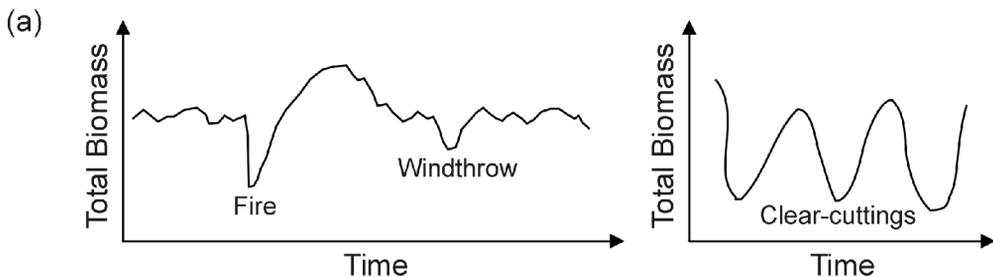


Figure 2 The steady-state mosaic is usually contextualized temporally – i.e., the relative abundance of different mosaic elements over time. On the left, the figure shows how the steady state might relate to 'natural' disturbances such as wildfire and windthrow, and on the right, how it might deviate from this pattern in landscapes undergoing change such as clearcutting. Nevertheless, as discussed in detail by Lertzman *et al.* (1998) and in the text, the steady-state mosaic also has an important component

Source: figure redrawn and adapted from Bormann and Likens (1979a) *American Scientist* 67, 660–69. Reprinted by permission of the *American Scientist*, magazine of Sigma XI, The Scientific Research Society

dynamics merely as an ever-repeating set of cycles, and the simple pulse stability viewpoint fails to incorporate several significant characteristics and implications of the presence of fire in the landscape. As discussed above, the landscape may be viewed as a collection of patches undergoing successional change. The character of these patches is a function of the frequency, intensity and spatial extent of the disturbance event(s) that led to their formation (White, 1979). Patches in a given state may be considered to have some probability of moving into an alternative successional state over some time period, either through succession or disturbance. If the problems involved with dividing landscape states into discrete stages are ignored, and the transition probabilities are assumed to be fixed (stationary), then the equilibrium frequency distribution of states in the landscape can be easily calculated through simple matrix algebra (e.g., as a simple transition matrix or Markov model, such as that of Horn, 1975). However, the dynamics of the landscape are far more complex than this. The pivotal assumption that the transition probabilities are temporally invariable is extremely unlikely to be realized. The periodicity of disturbance events is unlikely to be totally determined by changes in landscape structure resulting from succession (Christensen, 1993). External events such as climate and ignition events are also likely to be important. A further complication arises if some, or all, of the transitions have spatial dependencies. There are two general types of spatial dependencies relevant to landscape change: spatial covariation and neighbourhood effects. Spatial covariates encompass those dependencies related to soil type, topographic position or other environmental variables measured at a given point, while neighbourhood effects are those whereby the transitions at a given point depend on conditions in the cells surrounding that point, as is the case for the spread of contagious disturbances, for example. Spatial legacy effects, in which the history of a site affects present-day dynamics are also important. For example, Foster (1992) found different successional pathways based on site history (e.g., succession on abandoned pasture differed from that on tilled old fields), although this is a temporal legacy to some extent also.

Empirical studies also suggest that it is rare for landscapes to be at 'equilibrium'. For example, in Romme's (1982) study of landscape dynamics in Yellowstone National Park it was found that over a 200-year period the landscape fluctuated markedly in terms of composition and diversity. Romme (1982) concluded that this landscape may best be considered as a nonsteady-state system characterized by long-term changes in structure and function (as opposed to the shifting-mosaic steady-state proposed by Bormann and Likens, 1979b). Romme (1982) comments that these changes are the result of large fires that, with an approximate return interval of 300 years, periodically burn much of the area. Romme and Despain (1989) found that even if the study area was increased to nearly 130 000 ha the patch mosaic structure still showed evidence of large fluctuations over the last 250 years. Similarly, Baker (1989a, b) tested for a stable mosaic structure in an area in excess of 400 000 ha in the fire-influenced Boundary Waters Canoe Area (Minnesota) but found no evidence for a stable spatial structure at any of the five spatial scales used. He suggests that the lack of a steady-state mosaic is first the result of spatial heterogeneity in the fire-patch regime and second of a mismatch in the scales of fire patches and environmental heterogeneity.

It is also likely that rare, but very large, disturbance events are extremely influential in determining landscape dynamics (Turner *et al.*, 1998). All disturbance regimes have a size distribution, and characterizing the frequency-size structure of the disturbance

regime is important if landscape dynamics are to be understood, and landscapes are to be managed effectively (Baker, 1992). For example, Runkle (1981, 1982) found that although the average gap size in hardwood forests in the eastern USA was around 30 m², canopy openings might be as large as 1490 m², and that gaps of greater than 400 m² comprised about 1% of the landscape. Similarly, Strauss *et al.* (1989) estimate that in the boreal forest, less than 1% of all fire events account for more than 99% of the total burnt area (see also Malamud *et al.*, 1999). In the Boundary Waters Canoe Area, Baker (1989a, b) concluded that the size of the largest patch (i.e., extent of the largest disturbance) was more important than the mean disturbance size in determining the stability of the landscape.

So, for both theoretical reasons and from the evidence provided by empirical studies, concepts such as the steady-state shifting mosaic appear problematic when applied to landscapes subject to recurrent disturbance (Turner *et al.*, 1993). First, they seem applicable only to those systems where disturbances are small and frequent in a large area of relatively uniform habitat (Pickett and White, 1985b). DeAngelis and Waterhouse (1987) suggest that large areas may be more likely to exhibit a stable mosaic than small areas. Shugart and West (1981) found in a simulation-based approach that a 'steady' landscape was only likely where the area of the landscape was 50-times the average area of disturbance. However, Baker (1989b) failed to find evidence of a steady mosaic in a landscape 85-times larger than the average disturbance size, despite testing for it over a wide range of spatial scales. Baker (1992) comments that the probable reason for this disparity is that the size of disturbances was fixed in Shugart and West's (1981) model; variation in the size of individual disturbance events is sufficient to cause landscape structure to fluctuate over time. Second, steady-state concepts assume that the effects of any environmental discontinuities and gradients that may influence disturbance frequency are averaged across the landscape. Third, the definition of the temporal and spatial scales over which the aggregate mosaic should be considered is difficult (Turner *et al.*, 1993; Friedel, 1994). It is obvious that at small spatial scales (e.g., a few individuals) no equilibrium is likely to exist. However, the spatial scale can not be expanded infinitely; as the spatial scale approaches the biome level, concepts of equilibrium may become irrelevant. The same problems are also true in defining the temporal scale. It is conceivable that at some intermediate scale landscapes could be in a steady-state shifting mosaic condition, especially when there are strong feedbacks influencing the disturbance regime (White and Pickett, 1985; Turner *et al.*, 1993).

It would appear that most landscapes are rarely (if ever) in any form of stable equilibrium. Should this be the case, what are the main factors that prevent a landscape being in an equilibrium condition? Where individual disturbances affect a relatively large proportion of the landscape, it seems improbable that the landscape will ever be able to attain any sort of equilibrium (Sprugel, 1991). There will inevitably be large shifts from one time period to the next in the composition and structure of the landscape. An example of such a landscape may be the *Pinus ponderosa* (Pinaceae) forests of the western USA. In pre-settlement times individual fires may have covered hundreds of thousands of hectares in these landscapes, resulting in a dynamic mosaic with significant changes in species populations and rates of ecological processes as the relative proportion of different aged patches changed (Shinneman and Baker, 1997). Such dynamism in the landscape leads one to ask exactly what 'natural' might mean in such a system (Sprugel, 1991). A second possible cause of disequilibrium in landscapes

is single events (either natural or anthropogenic) that have long-lasting effects on the vegetation. For example, in the mid-Holocene, a 'new' pathogen of the eastern Hemlock (*Tsuga canadensis*; Pinaceae) caused an abrupt decline in populations of the species across its range; it took 1000–2000 years for most populations to return to their pre-decline levels (Fuller, 1998). Finally, climatic variability may preclude landscapes from reaching any sort of equilibrium. Substantial natural climate changes, large enough to cause significant changes in vegetation distributions, may occur on timescales well within the lifespan of many forest species (Delcourt *et al.*, 1982; Davis, 1984). Shugart (1984) has described some of the characteristics of equilibrium and disequilibrium in dynamic landscapes, and these are summarized in Table 1.

In an insightful discussion of the issues of landscape equilibrium Turner *et al.* (1993) propose a wider view of landscape dynamics which considers the spatio-temporal nature of disturbance and resultant landscape dynamics. They use four key components of the disturbance regime to characterize landscape dynamics: (i) disturbance frequency (or its inverse, return interval), (ii) rate of recovery from disturbance, (iii) the size or spatial extent of the disturbance, and (iv) the size or spatial extent of the landscape. These four descriptors may be distilled into two key parameters, one temporal and one spatial: T (the temporal parameter) is defined as the ratio of the disturbance interval to the recovery time. Three qualitatively different conditions exist for T : (i) disturbance interval is longer than recovery time ($T > 1$), (ii) the disturbance interval is the same as the recovery time ($T = 1$), and (iii) the disturbance interval is shorter than the recovery time ($T < 1$). S (the spatial parameter) is defined as the ratio of the size of the disturbance to the size of the landscape. There are two qualitatively different states for S : (i) disturbances that are large relative to the size of the landscape, and (ii) disturbances small relative to the size of the landscape. Turner *et al.* (1993) only consider those cases where $0 < S \leq 1$ (when $S > 1$ then the landscape is essentially too small to characterize the effect and recovery from disturbance).

Using a simple spatial simulation model and systematically exploring the interaction(s) between T and S , Turner *et al.* (1993) identified six qualitatively different regions of landscape dynamics (in terms of mean and variability of the landscape covered by each possible vegetation state) within the S – T state space (Figure 3).

The regions are based on the standard deviations (over time) of the amount of 'mature' vegetation in the landscape. The variability is small in area 'A' in Figure 3(a) because the landscape is dominated by mature vegetation since it is relatively

Table 1 Some characteristics of equilibrium and disequilibrium landscapes

Characteristic	Disequilibrium landscape	Equilibrium landscape
Disturbance size	Large	Small
Disturbance frequency	Small	Large
Vegetation age structure	Even-aged for frequent disturbances	All-aged
Total landscape biomass	Unpredictable	Regular
Population age distribution	Unstable for long-lived organisms	Stable

Source: from Shugart, 1984: 164. Reprinted by kind permission of Springer-Verlag.

undisturbed (high T and low S). Correspondingly, the variation is low in area 'B' because disturbances are so large and frequent that very little of the landscape contains mature vegetation. A landscape may also appear relatively stable, exhibiting low variance in the proportion of each vegetation type in the landscape, if disturbances are still relatively infrequent but disturbance events are larger. In this case a stable system with low variance in which much of the landscape is still occupied by late successional

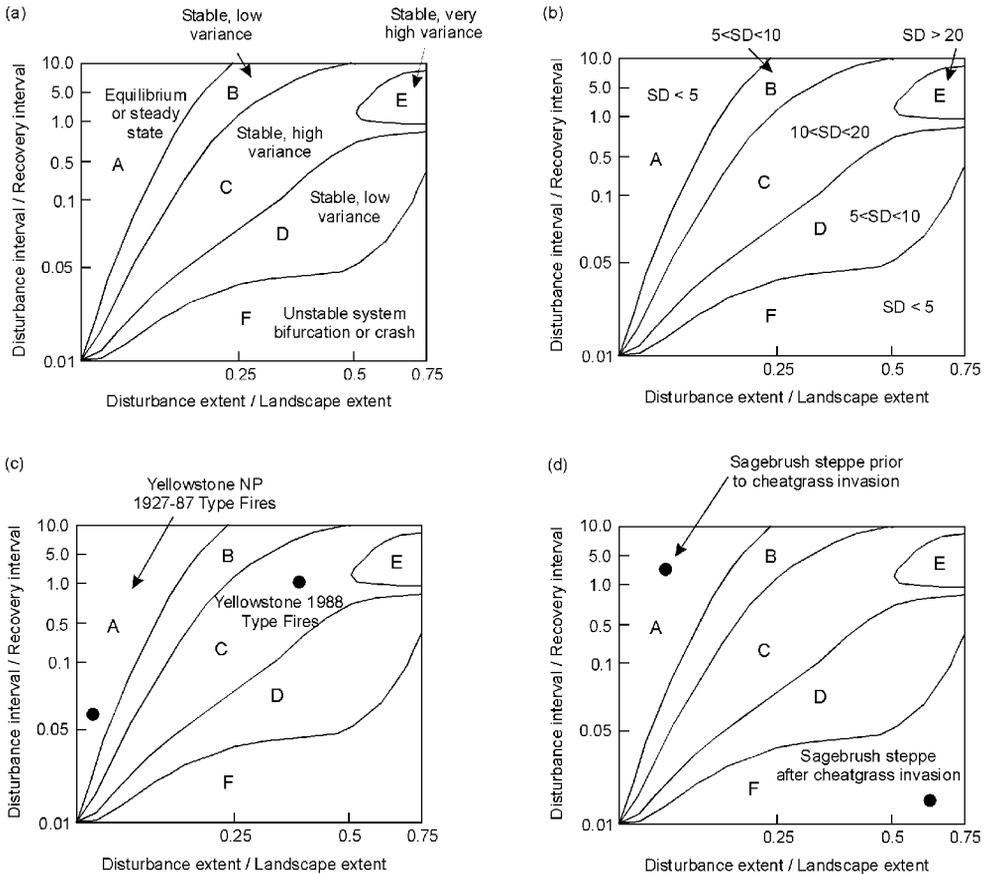


Figure 3 State–space diagrams of the temporal and spatial disturbance parameters used to describe potential disturbance dynamics. (a) Illustrates the six qualitatively different landscape dynamics; (b) a state–space diagram illustrating how the six regions correspond to standard deviation (SD) values for the proportion of mature vegetation in the landscape (from replicated model results); (c) an application of the state–space figure to the historical fires in Yellowstone National Park; and (d) an application of the figure to the dynamics of fire in sagebrush steppe before and after cheatgrass invasion

Source: redrawn after Turner *et al.*, 1993. Reprinted by kind permission of Kluwer Academic Publishers

vegetation is likely to ensue. The landscape may also appear stable with low variance when disturbances increase in size even further, although early successional stages will dominate. The landscape may be stable (*sensu* Loucks, 1970) but show very high variance with intermediate values of S and T , and show very high variance when $S > 0.5$, and the disturbance interval is long. Landscapes in this region of the S - T state space would probably be perceived to be disequilibrium systems. Turner *et al.* (1993) apply this qualitative categorization of landscape dynamics to a number of real-world examples (e.g., fire in Yellowstone National Park – Figure 3(c) – and changes to fire regime in semi-arid shrub-dominated ecosystems – Figure 3(d)), based on their disturbance regime. Landscape equilibrium can be expected when disturbances are small and disturbance intervals are longer, on average, than the recovery time (see also Table 1).

An interesting scenario suggested by Turner *et al.* (1993) is the potential for unstable or catastrophic change under conditions of frequent, large disturbance. If disturbances are sufficiently large and/or frequent, the landscape might not recover to the pre-perturbation trajectory. An alternative system trajectory may exist, and the disturbance could fundamentally change the nature of the system if certain components (species) cannot re-establish (see also Kay, 1991; Wilson and Agnew, 1992). It should be noted, however, that since the new trajectory(ies) cannot be predicted by the model, such a scenario cannot be illustrated as an outcome of the model.

The inherent variability in ecological systems has also begun to be recognized by land managers in the concept of 'historical variability' (Landres *et al.*, 1999). The use of natural variability for management focuses on two concepts: that past conditions and processes provide a context for managing ecological systems, and that disturbance-driven spatial and temporal variability is important in the majority of ecological systems. Landres (1999: 1179) emphasizes the scale-dependent nature of the concept stating that 'no *a priori* time period or spatial extent should be used in defining natural variability'. Wimberly *et al.* (2000) use a spatial landscape model and paleoecological data to examine the historical variability in old-growth forest in the Oregon Coast Range. They found that the historical age-class distribution was variable with the level of variability increasing as spatial extent decreased. Simulated old-growth land cover percentages were between 25 and 75% at the province scale (2.25 million ha) but increased to between 0 and 100% at the reserve scale (0.4 million ha). Wimberly *et al.* (2000) comment that in systems where the disturbance regime is characterized by large, infrequent disturbance events, management based on natural variability may only be feasible over large spatial scales.

3 Self-organization and positive feedbacks in disturbed landscape

A final, intriguing possibility is that ecosystems are self-organized across a range of hierarchical levels, including the landscape (Holling, 1992; Holling *et al.*, 1996), due, in part, to the 'memory' of the ecological system. In this context memory refers to the way in which the past history of the system affects its present structure and behaviour (and is therefore intertwined with the two-way feedbacks between pattern and process described above). Padiśák (1992) notes that the existence of 'memory' in ecosystems (at a number of scales) has long been implicit in ecology and is central to a number of

theoretical concepts (e.g., the storage effect of Warner and Chesson, 1985). A number of biologically plausible mathematical models (e.g., Satoh, 1990; Johnson, 1997) have shown that small-scale ecological interactions can cause the emergence of dynamic, coherent, large-scale spatial patterns. This process is the essence of self-organization (Rohani *et al.*, 1997). Such models suggest that spatial structure may evolve even where there is an absence of external forcing heterogeneity, and has led to the suggestion that at least part of the spatial complexity seen in ecological systems can arise from deterministic origins (Bascompte and Solé, 1995). This view has, however, been criticized on the grounds that the emergence of system organization may be an artefact of the simplicity of the models being used (see Bascompte and Solé, 1998). Nevertheless, spatial self-organization has evolved even in models incorporating stochastic terms and, in some cases, the maintenance of spatial structure is dependent on some level of noise or stochasticity (Rohani *et al.*, 1997).

Holling *et al.* (1996) describe a series of simulation experiments designed to examine how memory may lead to self-organization in disturbed landscapes. Four models were constructed in which the spread of fire in a forested landscape was simulated. In the first model flammability was independent of forest age (time since last disturbance) and, in the other three, flammability was dependent upon forest age and other refinements were progressively added. Thus, in the first model the system has no memory (as defined above) whereas in the others it does. Although the landscape dynamics simulated in each of the four models were similar in some regards, one key result emerged. When flammability is a function of stand age past fires influence future fires and the landscape self-organizes itself into a self-sustaining, patchy mosaic even in the absence of external heterogeneity (such as topography). Such self-organization was not found in the memory-less system but was recurrent in the other three. Landscape self-organization occurred when fires produced a spatially structured landscape of persistent, even-aged patches. This self-organization, and the memory that causes it to emerge, occurs whenever fire spread is a function of previous fires (this is likely to hold for other comparable contagious disturbances). As a result landscape pattern greatly influences where fire burns in the future, thereby encouraging patch maintenance. Holling *et al.* (1996) found the emergence of this self-organized spatial structure to be very robust to changes in the parameterization of the system.

Comparable conclusions were drawn by Hendry and McGlade (1995) in an analysis of the role of memory in a model (described by Wissel, 1991, 1992) of cyclic succession in European beech forests. The beech forest system was found to be spatially structured if the ecological system had memory. In the absence of memory random spatial patterns evolved. Hendry and McGlade (1995: 159) comment that '... memory does not itself cause structure to emerge from the model's interactions, it amplifies other aggregating mechanisms within systems'. This appears to be a different interpretation of the role of memory from that of Holling *et al.* (1996) who attribute self-organization to the presence of memory in the system. Similarly, Wiegand *et al.* (1998) attribute cyclic spatial dynamics in a model of a South African shrubland ecosystem to the spatial memory embedded in the system.

Self-organization is driven in these model systems by the strong positive feedbacks between landscape pattern and ecological process. These feedbacks are made possible by the memory embedded in these systems (expressed as landscape pattern) and the way that this influences processes that are themselves agents of pattern formation.

Although largely explored through the use of spatial models, such feedbacks have been seen in the 'real' world. For example, Cochrane *et al.* (1999), describe how otherwise nonflammable vegetation (e.g., humid forest) may be changed rapidly through a positive feedback mechanism involving fire. In essence, the occurrence of any fire alters the vegetation such that it becomes more flammable and hence subsequent fires are more likely to spread.

IV New approaches and conclusions

Although it is clear that space and spatial heterogeneity are important across all scales, it remains unclear how best we can address the issue. Or, in other words, having accepted that we need to consider space in theoretical and empirical studies, how should we do this? Many approaches may be taken to the analysis of space. For example we can obtain (often at considerable cost) spatial coordinates (x, y, z) for all individuals in a population or community, or we can use cellular automata (CAM) approximates, spatially implicit models (see, for example, Levins, 1969) or nonspatial approaches. Running parallel to this spatial 'gradient', there are clearly a series of tractability–realism tradeoffs; each approach provides new insights into the role of space in ecological dynamics, but it also brings its own limitations. Whereas simple models may be analytically tractable they are often criticized on the grounds of 'lack of realism', conversely, detailed CAM may be ecologically very realistic but sacrifice analytic tractability.

Comparison of nonspatial (or spatially implicit) and spatially explicit models of the same system have shown some interesting results. For example, Tilman *et al.* (1997) and Holmes (1997) have compared spatially implicit and explicit models (of a patch occupancy system and the Kermack–McKendrick epidemic model, respectively). Comparison of the two different formulations shows how the inclusion of space alters potential equilibriums in such systems (equilibriums are analytically solvable in the spatially implicit versions of the model and are estimated using Monte Carlo methods in the stochastic, spatially explicit forms). The spatially explicit model of Tilman *et al.* (1997) also shows how spatial pattern may arise through simple spatial processes such as neighbourhood dispersal, even in the absence of underlying environmental heterogeneity. Such tests could be carried out to look at equilibrium in disturbed landscapes. For example, simple Markov or differential models of landscape dynamics (Shugart *et al.*, 1973; Calder *et al.*, 1992) could be compared with spatially explicit landscape models representing the same systems. For the reasons outlined above (Section III,2) these alternate conceptualizations would no doubt yield very different results; whereas a Markov model will always predict a steady-state equilibrium, such a state may never be reached in a stochastic, spatially explicit model. New approaches such as the 'pair approximations' described by Hiebeler (1997, 2000) have potential as a way of bridging the gap between mean-field or spatially implicit models and spatially explicit simulations. They, and other such sophisticated techniques, may also help provide insight into the circumstances when nonspatial approaches and approximations break down. Comparison of spatial and nonspatial (or spatially implicit) models is one way in which the role of space in driving ecological dynamics can be investigated.

Spatial approaches such as those outlined above promise to link the spatial hetero-

geneity we see at multiple scales with ideas of (non)equilibrium and (in)stability. However, as highlighted by Steinberg and Kareiva (1997) it has proved difficult to link spatial theory and empirical ('real-world') observations. A wealth of spatial ecological theory has been produced over the last two decades, much of which remains untested (and some of which is formulated in such a way as to be untestable). Steinberg and Kareiva (1997) describe two approaches to empirically evaluating spatial theory. First, a specific model may be parameterized and then the predictions of that model quantitatively addressed. This approach is not often followed and Steinberg and Kareiva (1997) suggest this is due to a reluctance to place faith in a single complex model. Second, a general prediction can be tested without reference to a specific model. This approach is plagued by problems of replication, statistical power and scale. In most cases, it is inevitable that clear-cut manipulative experiments will have low power and suffer from problems such as the definition of terms such as stability or equilibrium. Many spatial landscape issues are very hard to test, as they are contingent on extremely rare and hard to document events occurring (for example, long-distance dispersal is thought to be pivotal in invasion). A further problem is the tests are often ambiguous: it is often unclear whether their outcomes represent a 'real-world' effect or are an artefact of the designs/scales used in the experiments. Nevertheless, many other areas of ecological theory remain difficult to test empirically and this does not, of itself, make them any less scientific or reasonable. Where experiments have been carefully designed (and new analytical methods developed) interesting results have been found. Yu *et al.* (2001), for example, test the idea that species coexistence in a homogenous habitat may be promoted by spatial structure by testing spatial models of coexistence with empirical data. More such studies are required if the wealth of spatial theory developed is to be effectively used.

Ecologists have long ignored space but over the last two decades this has changed. In part this burgeoning interest in space and spatial pattern has been driven by developments in analytical techniques, but it is also, to some degree, an outcome of a change in the way in which the idea of 'equilibrium' in ecosystems has altered. It has been realized that space can fundamentally alter the dynamics and outcomes of ecological processes. This has largely been achieved through theoretical, model-based studies; the challenge remains to empirically test and explore the large body of spatial ecological theory developed over the last 15–20 years.

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